FUNCTIONAL INTEGRITY OF PLANT–POLLINATOR COMMUNITIES IN RESTORED HABITATS IN MAURITIUS

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THIS THESIS IS DEDICATED TO MY PARENTS AND GRANDPARENTS

FOR THEIR LOVE AND SUPPORT

CONTENTS

CHAPTER 1

General introduction

Habitat restoration in Mauritius

The oceanic island of Mauritius, which belongs to the Mascarene archipelago, is situated some 800 km east of Madagascar in the south-western Indian Ocean between 19°50'S and 20°51'S, and 57°18' and 57°48'E (Fig. 1a), and has a land area of 1865km^2. Mauritius' unique and diverse fauna and flora have been subject to a wave of extinctions since human colonisation about 400 years ago, a pattern typical of many island ecosystems. The primary forces driving these extinctions have been, and continue to be, habitat destruction, fragmentation and degradation by invasive alien plant and animal species (Mauremootoo *et al.* in press-a). As a result, only about 1.9% of Mauritius is covered in the native Mauritian forest today (> 50% native canopy), the rest of the island's forest cover is either plantation forestry or native forest heavily degraded by introduced plant species (Fig. 1b; Page & d'Argent 1997). Currently, 94% of flowering plant species endemic to Mauritius is threatened to some degree according to IUCN criteria (Mauremootoo *et al.* in press-b) making the flora of Mauritius one of the most threatened island floras in the world. Both habitat degradation and vertebrate extinction have been covered in great detail elsewhere (Vaughan & Wiehe 1941, Lorence & Sussman 1986, Cheke 1987, Strahm 1994, Cheke & Hume in press, Mauremootoo *et al.* in press-a). However, very little is known about the invertebrate diversity of Mauritius. Species inventories on some selected invertebrate groups exist (Vinson 1938, Williams 1981, 1982, 1983, 1989, Griffiths 2000) and a list of economically important, introduced invertebrate species has been compiled (Williams & Ganeshan 1999), but this work is far from complete. Given such lack of basic taxonomic information on many invertebrate groups, we can only speculate about the conservation status and the probable decline of invertebrate diversity in Mauritius.

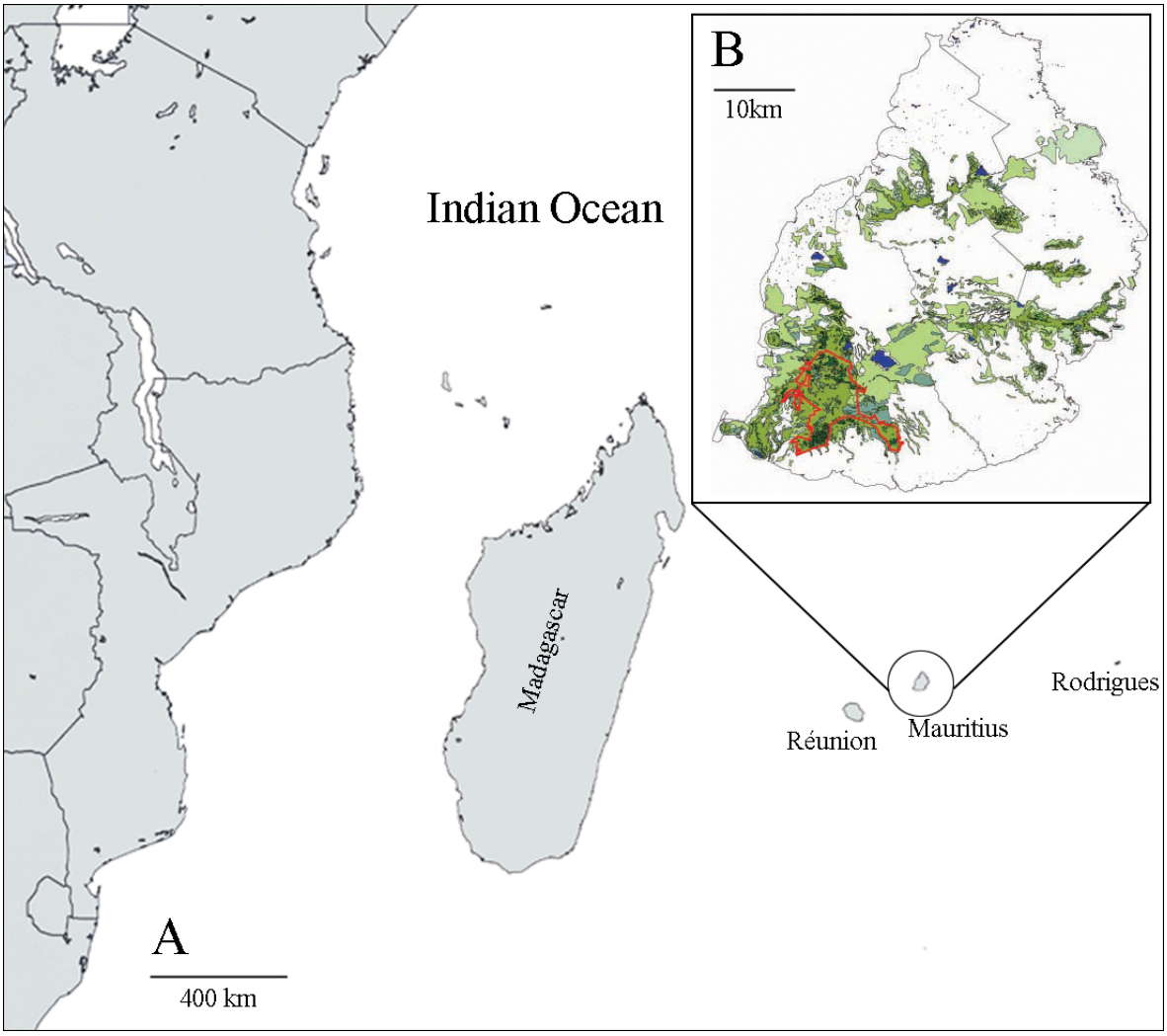

Figure 1 (A) The Mascarene archipelago includes the islands of Réunion, Mauritius and Rodrigues, which are located between approximately 600 and 1300km east of Madagascar in the south-western Indian Ocean. The inset (B) shows the forest on the island of Mauritius. The Black River Gorges National Park is outlined in red. Different shades of light green reflect different level of invadedness, and light blue areas show plantation forest. Dark green areas depict the last remnants of native vegetation (forest with >50% native canopy) (Source inset: Mauritian Wildlife Foundation, 2006).

The current knowledge of Mauritian biodiversity reflects the focus of conservation management on single-species recovery programmes of large vertebrate species in Mauritius. Much traditional conservation effort and resources have gone into saving target species such as the Mauritius kestrel *Falco punctatus*, the pink pigeon *Columba mayeri*, the echo parakeet *Psittacula eques* and the Mauritius fody *Foudia rubra* from the brink of extinction. More recently, more resources have been directed towards plant restoration schemes, the most significant of which is a network of 11 conservation management areas (CMAs) covering 44ha in the south west of the island. This network was set up by the Government conservation service in collaboration with the non-governmental Mauritian Wildlife Foundation (Mauremootoo *et al.* in press-b). CMAs are fenced – against deer and pigs – plots of various sizes (0.1–24 ha) where introduced plant species are hand-weeded twice a year. This management aims to preserve a representative sample of the native flora. If fences are maintained in good condition, regeneration of native forest does occur. For example, in Brise Fér Old Plot, a CMA initially weeded in 1987, the efforts have resulted in a slow but gradual regeneration of 53–68% of native plant species compared to 32–40% in a comparable unrestored, degraded area (Mauremootoo *et al.* in press-b). As habitat restoration in Mauritius aims to restore whole ecosystem functioning it is crucial to determine whether this type of management also benefits the native, co-adapted animals. However, most native plant species rely on mutualistic interactions, such as pollination and seed dispersal, for successful regeneration, and it is not known whether these ecosystem functions are being fulfilled by the extant fauna. Habitat restoration can only be successful in the long-term when natural plant reproduction is ensured, and the absence of native mutualists may severely threaten this restoration aim.

In this thesis, I compare plant–animal interactions of restored and unrestored, heavily degraded areas to increase our understanding on how invaders alter plants' interactions.

Pollination studies: from single species to community approach

Just as conservation schemes in Mauritius are moving from a single species focus to a more holistic approach, pollination biology is also following the same route. Pollination biologists have long been focusing on the reproductive biology of single plant species and their interactions with an array of pollinators. Those often meticulously conducted studies have provided detailed and valuable insights into the pollination ecology of many intriguing floral systems, and the increasing knowledge of these systems has sparked a debate on the role of generalisation in plant–pollinator interactions (Herrera 1988, 1996, Ollerton 1996, Waser *et*

al. 1996, Johnson & Steiner 2000). While the search for evolutionary and ecological mechanisms behind generalisation in pollination systems is ongoing, researchers have started to embrace this new understanding by applying whole community approaches when studying plant–pollinator interactions, both qualitatively (Arroyo *et al.* 1982, Motten 1986) and quantitatively (Memmott 1999, Gibson *et al.* 2006). In fact, pioneers carried out community-level studies as early as the 1920s (Robertson 1928, Clements & Long 1923, Moldenke 1975, Moldenke & Lincoln 1979), but the dramatic increase in technology since has fuelled the return to such approaches. Although community studies overlook the detailed biology of specific interactions, such research has demonstrated some general patterns in the structure of plant–pollinator communities (Olesen & Jordano 2002, Jordano *et al.* 2006). This approach has attracted considerable recent scientific attention (Bascompte *et al.* 2006, Thompson 2006).

In my thesis I apply both approaches: I present observational and experimental studies on mutualistic and antagonistic plant–animal interactions both from the perspective of individual plant species and of entire communities.

Invasion on islands

While scientists have disagreed on whether island habitats are inherently more easily invaded (e.g. Cronk & Fuller 1995, Simberloff 1995), consensus is that exotic species appear to devastate island ecosystems more than mainland sites (D'Antonio & Dudley 1995, Whittaker 1998, Simberloff 2000). The latter is often explained by anthropogenic habitat destruction and over-exploitation, which destabilised many island ecosystems in the past and increased their susceptibility to the spread of introduced species (Didham *et al.* 2005). Introduced animal and plant species now account for a large proportion of island biotas (Cole *et al.* 1992, Henneman & Memmott 2001, Magee *et al.* 2001), and interactions between native and introduced species, both direct and indirect, are omnipresent in such ecosystems (e.g. Holway *et al.* 2002, O'Dowd *et al.* 2003, Ghazoul 2004, Mitchell *et al.* 2006). However, despite many recent studies on different aspects of invasion, e.g. introduced flower visitors competing with native pollinators for floral resources (e.g. Dupont *et al.* 2004) and introduced plants competing with native plants for pollination (e.g. Brown & Mitchell 2001), very little experimental work has been carried out on how introduced species influence plant–animal interactions at the community level.

In this thesis I present two experimental studies which shed light on the impact of invasive species on plant–animal interactions. In addition, the research presented here provides new insights into island invasion processes at a community level.

Concept and outline of the thesis

My thesis has two general aims: (1) to investigate mutualistic interactions, i.e. pollination and seed dispersal, in restored and unrestored sites in Mauritius and (2) to further understand the impact of introduced plant and animals on such mutualistic interactions. In order to address these issues, I employed several approaches including food web ecology, pollination ecology and experimental techniques to improve our fundamental understanding of complex community interactions for conservation management. As with applied conservation in Mauritius, which has broadened from single-species recovery programmes to now include ecosystem restoration, and pollination ecology, which developed from focussing on single plant species to habitat approaches, my work presents findings on a range of scales: from detailed observational studies on single plant species supplemented by in-depth field experiments, to an extensive community-wide study of entire plant–pollinator systems. Specifically, my thesis contains the following chapters:

Chapters 2 and 3 contain detailed observational and experimental data on the pollination and seed dispersal ecology of the endangered endemic *Syzygium mamillatum*, which occurs in a small population inside and outside a restored area of upland moist forest in Mauritius. In Chapter 2, we highlight the effect of habitat restoration on pollination interactions and reproductive traits of the cauliflorous *S. mamillatum*. In Chapter 3, we test ecological analogue seed-dispersing species as potential replacements for extinct animals and provide the first experimental investigation of the Janzen–Connell model for seedling establishment on oceanic islands.

Chapter 4 focuses on indirect interactions between invasive and native plant species mediated by shared pollinators. I conduct a removal experiment using the rare endemic *Bertiera zaluzania* and the introduced invasive strawberry guava *Psidium cattleianum* as our model system to investigate whether the rapid spread of invasive plant species has indirect effects on the reproductive success of native plant species.

Chapter 5 argues that growing crops in proximity to natural ecosystems to increase yield, a favoured approach in the tropics, has a potentially harmful flip-side, because crop pests can invade near-by habitats, switch hosts and cause damage to native or endemic plant species. We illustrate this with the impact of the introduced coffee pest *Prophantis*

smaragdina (Lepidoptera) on the reproductive output of the endemic *Bertiera zaluzania*, which occurs in the vicinity of coffee plantations.

Chapter 6 compiles extensive experimental community data on plant–pollinator visitation webs in restored and unrestored habitats in Mauritius; one site with only native plant species and a second comparable site, which is heavily degraded by invasive alien plant species. This chapter breaks new ground in pollination ecology by presenting fully quantified visitation webs on two entire flowering plant communities throughout the main flowering season. Additional detailed information on plant phenology, plant reproductive performance and each pollinator species furthers our understanding on the effects of habitat restoration on plant–pollinator systems and the invasion of animal species in an upland pollinator community in Mauritius.

In *Chapter 7*, I make use of the high temporal and spatial resolution of the visitation webs presented in Chapter 6 and investigate changes in network properties over time. Throughout the season, plants and pollinators 'join' and 'leave' the network of interactions, and this may have consequences for the inherent structure of pollination networks.

Most chapters are written in manuscript format, which will inevitably result in some overlap among them. However, Chapter 6 contains information for several manuscripts which were pooled to avoid repetition.

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CHAPTER 2

Habitat structure affects reproductive success of the rare endemic tree *Syzygium mamillatum* (Myrtaceae) in restored and unrestored sites in Mauritius

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(submitted to Biotropica)

ABSTRACT

Invasive alien plants affect the functioning of ecosystems by altering plant–animal interactions, such as pollination, which may impede natural regeneration of native plant species. In Mauritius, we studied the reproductive traits and pollination ecology of the rare endemic cauliflorous tree *Syzygium mamillatum* in a restored forest (all alien plant species removed) and an adjacent unrestored area (degraded by invasive plants). Flowers of *S. mamillatum* were only visited by generalist bird species. Although the initial number of flower buds per tree in the restored forest tended to be higher than that of trees in the unrestored area, final fruit set and the number of seeds per fruit were lower in the restored forest. This corresponded with lower bird visitation rates in the restored area. Additionally, in budding stage most trees were severely attacked by lepidopteran larvae, and bud loss through herbivory was higher in the restored forest. Thus, the difference in reproductive performance of *S. mamillatum* between the two localities was caused by contrasting herbivorous attack and bird visitation behavior in restored and unrestored areas. Our findings illustrate the importance in restoration efforts of mimicking original physical structure of habitats and interaction structure of interspecific relationships, and the difficulty of doing so given the imperfect knowledge and the reality that many native species have become locally extinct and replaced by exotic species.

INTRODUCTION

Islands are often described as biodiversity hot-spots due to their relatively high levels of endemism and their disproportional contribution to global species diversity (Whittaker 1998, Myers *et al.* 2000). Invasive alien species, however, threaten the extant native biological diversity of island ecosystems (Cheke 1987, Simberloff 1995, Fritts & Rodda 1998, Valido *et al.* 2002). Introduced species may interact with native species in several ways: many compete with natives for resources (Callaway & Aschehoug 2000, Daehler 2003) or benefit from mutualistic interactions with resident species, often to the detriment of native mutualisms (Bond 1994, Simberloff & von Holle 1999, Richardson *et al.* 2000, Ghazoul 2002). Thus invasive alien plant species can disrupt native plant–animal interactions critical for plant reproduction, such as pollination, by reducing relative abundance or density of native plant populations (Ghazoul 2005, Ward & Johnson 2005), and by altering pollinator behavior (Brown & Mitchell 2001, Chittka & Schürkens 2001, Ghazoul 2004). Where populations are already compromised through habitat destruction, as is often the case on islands, this might lead to localized extinction of plant or native pollinator populations, though this has yet to be demonstrated conclusively.

The continuing decline of native plant and animal species in Mauritius, following the initial human-caused destruction of natural habitats, has been ascribed primarily to the spread of introduced invasive species (Mauremootoo *et al.* in press-a), which now dominate the remaining upland forests (Vaughan & Wiehe 1941, Lorence & Sussman 1986, Cheke 1987). Today, only about 2% of Mauritius is covered with some degree of native forest (Page & d'Argent 1997), and even these remnants are seriously degraded in most areas. The original Mauritian fauna comprised a range of potential pollinating and seed-dispersing avian species, many of which are now locally or globally extinct. The loss of these native mutualists may limit the natural regeneration of native plants that once were dependent on them. Consequently, the remaining populations of Mauritian plants may be vulnerable to both the direct impacts of invasive plants and the disruption of their reproductive systems through extinction of their mutualistic partners as well as competition with invasive plants for extant pollinators and seed dispersers.

To restore patches of native plant communities in Mauritius, the National Parks and Conservation Service (NPCS) has established several Conservation Management Areas (CMAs) since 1969, representing remnants of the major original habitat types. These areas are fenced to exclude deer and feral pigs, and are regularly hand-weeded to eradicate invasive plant species. A survey in one of these CMAs (Brise Fér 'Old Plot', 1.26 ha) eight years after

the start of restoration work in 1987 showed improved natural regeneration of native flora compared to adjacent unrestored areas (Mauremootoo *et al.* in press-b). Thus, although there is evidence that the original plant community can regenerate following restoration, information on what actually limits regeneration of endemic plants in unrestored habitats is lacking. To improve current restoration strategies, it is necessary to understand the mechanistic basis of recruitment success. In our system, abundant invasive plant species may have disrupted native recruitment through the pollination process, and the removal of alien plants may therefore facilitate native recruitment through the recovery of this process.

In this study, we investigated the effects of habitat restoration on pollination interactions and fruit/seed set of the rare endemic tree *Syzygium mamillatum* Bosser & Guého (Myrtaceae) in a CMA and an adjacent unrestored area. *Syzygium mamillatum* is cauliflorous with flowers developing directly on the trunk. Cauliflory is a characteristic feature of many trees in Mauritius (Bosser *et al.* 1983) and elsewhere in the tropics (Endress 1994). No information is available on the pollination of *S. mamillatum*, but the congeneric *S. mauritianum* Guého & Scott with similar pink, showy flowers is primarily visited by nectarivorous birds (D. M. Hansen, pers. obs.). Based on these observations and the assumption that pollinator visitation may be negatively affected by invasives and restored by habitat management, we made two predictions: (1) due to eradication of invasive plants and regular weeding in the CMA, the flowers of *S. mamillatum* trees will be more conspicuous to bird pollinators than those of trees in the unrestored areas, and will therefore attract more pollinator visits; and (2) increased flower-visitation rate in the CMA will result in higher fruit and seed production in comparison with plants in the unrestored area. Lastly, preliminary observations indicated that flower buds at both sites were being attacked by a herbivorous lepidopteran larvae. Therefore, we studied the impact of floral herbivory on the reproductive success of *S. mamillatum* at a restored and unrestored site.

METHODS

Study area

We conducted the study in the Black River Gorges National Park in Mauritius between July 2003 and January 2004. Our study site was Brise Fér CMA (24 ha, 20°22′ S, 57°26′ E, 570–600 m asl), established in 1996. The native tree community in the restored (CMA) and adjacent unrestored area of Brise Fér consists mainly of canopy trees of the families Burseraceae, Ebenaceae, Celastraceae and Sapotaceae, and several sub-canopy trees of the genera *Gaertnera* (Rubiaceae) and *Syzygium* (Myrtaceae) (Strahm 1994). In the unrestored

area, invasive plants, primarily guava *Psidium cattleianum* Sabine (Myrtaceae), privet *Ligustrum robustum* (Rox.) Blume (Oleaceae), and several weedy Melastomataceae, form an impenetrable understorey with a canopy of about 3–5 m in height. Native trees are found scattered within this site (see also Lorence & Sussman 1986).

Study species

During our initial survey in July and August 2003 we found a total of 120 mature trees of *S. mamillatum* in the Brise Fér area (previous surveys suggested only 20 extant individuals of this species; G. d'Argent, pers. comm.). *Syzygium mamillatum* is endemic to Mauritius and the recorded individuals represent the last extant population, accounting for 87% of all the mature trees of this species. The remaining 18 trees are either isolated individuals or small stands located within the boundaries of the National Park (M. Allet & J.-C. Sevathian, pers. comm.). Eighty-two mature healthy trees in the CMA and 38 in the unrestored area were labeled, mapped, and included in our study. Since we worked with the only extant population, replication across several sites was not possible. Instead almost the entire population of this rare species was sampled to estimate population parameters. Nevertheless, we recognize the potential for within-site non-independence of the data and tested for spatial autocorrelation using Mantel tests (see below). Furthermore, we felt it was justified to investigate the effects of conservation interventions despite limited potential for site replication, precisely because *S. mamillatum* is endangered, but also because this species exemplifies the fate of many other endangered endemic tree species.

Syzygium mamillatum grows to 6–9 m in height and is part of the sub-canopy strata of the native forest. The trees show a spectacular display of numerous, hermaphroditic flowers (calyx tube 8–10 mm long) on the trunk (Fig. 1a), located within 50 cm of the ground (Fig. 1b). The flowers contain nectar and are scentless. Each flower displays a hemispherical array of 80–90 anthers (filament length 8–10 mm), contains 15–20 ovules (Scott 1990), and produces a large and fleshy fruit. Preliminary experimental data suggested that *S. mamillatum* is largely self-incompatible (4% fruit set from 107 bagged flowers on 7 plants; C.N. Kaiser unpublished data), as is the case for many arborescent Myrtaceae species (Lack & Kevan 1984, Beardsell *et al.* 1993, Proenca & Gibbs 1994). In 2003, *S. mamillatum* flowered from November to December.

Habitat structure

Before restoration, Brise Fér CMA was as degraded as the unrestored area (Strahm 1994) but since weeding began in 1996, native plant species have been slowly regenerating. As a result of restoration, the forest understorey in the CMA is now very open and little vegetation obstructs the floral display on tree trunks. In contrast, flowers on trees in the adjacent unrestored area are hidden from a human observer's view by a dense understorey of invasive plants. To investigate and quantify the differences in habitat structure, we measured tree density around the focal trees. We counted the number of native and exotic trees (exceeding a diameter at breast height of 3 cm) within a radius of 3 m around *S. mamillatum* trees that were used for pollinator observations in the CMA and the unrestored area ($n = 9$ in each area).

Herbivory

During flower bud development (October–November 2003) many *S. mamillatum* trees were attacked by the larvae of *Polyhymno* sp. (Lepidoptera, Gelechiidae; identified as an unknown species by Dr. Klaus Sattler, Natural History Museum London). Adult moths deposited their eggs in young flower buds and the developing larvae consumed the entire bud over a period of approximately one week. We assessed the impact of these attacks by counting affected trees in the population and affected buds per tree. The proportion of attacked buds was the number of destroyed buds divided by the initial total number of buds per tree. The spread of the herbivore through the tree population was monitored weekly during the budding time.

Pollinator observations

Between 12th November and 9th December 2003, pollinator observations were carried out on nine flowering trees in the restored and ten trees in the unrestored area in one-hour 'observation units' for a total of 15 h in each area. Each tree was observed for 1–3 h. Flowers opened not before 7.00 am and anthesis lasted for one day only, and thus all observations were carried out between 7.00 am and 7.00 pm. We spatially stratified observation trees across the population to cover the centre and the edges of the population evenly, and we selected those trees that had most flowers. Observations were carried out with binoculars (Leica 10 × 32) at a distance of larger than 6 m from the tree, which was considered far enough to avoid disturbing vertebrate flower visitors and sufficiently close to spot invertebrates. For each observed tree, we recorded the number of flowers observed, *i.e.*, visible on the trunk from our observation post (range: 18–450 flowers) and the total number of flowers displayed on the trunk. We recorded both visitation rate and 'bout length' of flower

visitors. Visitation rate is defined as the total number of visitors to the tree per hour divided by the number of visible flowers per tree. Bout length refers to the number of flowers probed per hour divided by the number of flowers observed.

To quantify the pollen load of avian flower visitors, we mistnetted birds for 12 h close to 12 trees in full blossom in the CMA. We caught a total of 25 birds, which were ringed before release to avoid re-sampling the same individuals. Pollen samples were collected by sweeping the forehead, breast and beak of each bird with a 25 mm^2 piece of basic fuchsin gel (Kearns & Inouye 1993). The sampled pollen grains were compared with a reference pollen collection (Kaiser 2006) and counted under a light microscope using a counting grid.

Plant morphometrics and reproductive performance

For 119 *S. mamillatum* trees, we measured diameter at breast height (dbh), tree height (H) (n = 112 trees), and mean distance to the nearest three conspecific neighbors (NND). We used Mantel statistics to investigate potential spatial autocorrelation for seed and fruit set (n = 119 trees), and visitation rate (n = 19 trees) (Sokal & Rohlf 1995). We calculated euclidean distances as dissimilarity indices for seed set, fruit set and visitation rate, and compared observed correlation coefficients with the reference distribution of correlation coefficients based on 1000 randomized permutations (Legendre & Legendre 1998).

Early in the season before larvae attacked the developing buds, we counted emerging buds (see Fig. 1b) to quantify initial flower bud production of all trees in the population. Fruit set was calculated for each tree as the number of developing fruits divided by the number of buds that developed into open flowers. Fruit counts were carried out for each individual tree at the end of December 2003, approximately 10 days after the trees had finished flowering. A second fruit count was conducted mid February 2004 to investigate a potential reduction in fruit production that could be caused by maternal fruit abortion (Stephenson 1981), late-acting self-incompatibility (Proença & Gibbs 1994) or early inbreeding depression (Nic Lughadha 1998). The difference in number of fruits per tree between the two surveys divided by the initial number of developing fruits per tree is a measure of fruit loss. We collected a total of 1291 mature fruits (33% of total fruit crop) from 34 trees in the restored and 21 trees in the unrestored area and determined average fruit size (widest diameter), fruit weight, number of seeds, and seed weight.

Data analysis

We used parametric tests when assumptions of normality could be met by transformation and applied appropriate non-parametric tests otherwise. We cube-root transformed visitation rates and bout lengths, and log-transformed plant morphometrics and reproductive parameters. Means across trees ± SE are given throughout unless otherwise noted.

To investigate the relationship between the amount of fruits lost between the two fruit counts and the initial number of fruits produced by each tree in both sites, we fitted a linear model with fruit loss as the response variable and the number of fruits per tree and site (restored/unrestored) as explanatory variables. Proportional data such as fruit set, bud and fruit loss were arcsine transformed to meet the assumptions of normality and homoscedasticity (Quinn & Keough 2002).

To predict the patterns of fruit set, seed set and bud loss in the restored and the unrestored site, we fitted three linear models. The response variables 'number of seeds per fruit', and 'proportion of buds per tree destroyed by herbivores' (bud loss) were fitted against the predictor variables 'mean number of buds per tree', 'mean nearest neighbor distance' (NND; both log-transformed), and site (restored/unrestored). To test whether pollinator visitation could predict fruit set, we replaced the predictor variable NND with 'visitation rate' in the third regression analysis. All analyses were conducted with the statistical package R.2.1.1 (R Development Core Team 2005)

RESULTS

Habitat structure

The density of native trees in the vicinity of *Syzygium mamillatum* was not significantly different between the CMA and the unrestored areas ($F_{1,16} = 0.278$, $p = 0.61$). However, the number of introduced trees within a 3 m radius of *S. mamillatum* trees in the unrestored area exceeded the number of native trees by a factor of six (restored: 18.7 ± 1.6 trees; unrestored: 109 ± 7.3 trees; $F_{1,16} = 187$, $p < 0.001$).

Herbivory

The first attacks of buds by *Polyhymno* sp were recorded on 18th November 2003 (approximately two weeks prior to first anthesis) in the CMA on only three trees located within 10 m of each other. Three weeks later, approximately 50% of all trees were severely affected. Attacked trees lost on average 47.7% (± 3.5) of their buds, 60.5% (± 4.0) in the restored and 28.4% (± 5.7) in the unrestored site. There was a significant positive correlation

between the number of buds per tree and the proportion of destroyed buds per tree ($r = 0.27$, $n = 69$, $p = 0.026$). Both the total number of buds destroyed by *Polyhymno* sp. and the proportion of buds destroyed per tree were higher in the CMA than in the unrestored area (number of buds destroyed: $F_{1,67} = 18.9$, $p < 0.001$; proportion of buds destroyed: $F_{1,67} = 14.8$, $p < 0.001$). Overall, the number of buds destroyed per tree was explained by management scheme, 'mean number of flowers' per tree and 'nearest neighbor distance' ($F_{3,65} = 5.93$, $p = 0.001$).

Pollinator observations

We observed a total of 89 interactions between flowering trees of *S. mamillatum* and three species of bird (Table 1). The endemic grey white-eye *Zosterops mauritianus* Gmelin (Zosteropidae) (Fig. 1c) was the most abundant flower visitor of *S. mamillatum* in the CMA and the unrestored forest, but we observed fewer individual birds in the unrestored area (Table 1). The number of individuals of the introduced red-whiskered bulbul *Pycnonotus jocosus* L. (Pycnonotidae) was small and similar in both areas. The endemic Mauritius bulbul *Hypsipetes olivaceus* Jardine & Selby (Pycnonotidae) was only observed at trees in the CMA. Pollen swabs taken from one mist-netted Madagascar fody *Foudia madagascariensis* L. (Passeridae) revealed that this species may be a pollen vector for *S. mamillatum* although it was not observed visiting flowers of *S. mamillatum*. Pollen from *S. mamillatum* was indistinguishable from pollen of other species in the genus using light microscopy. Thus, we could not assume that every pollen grain counted belonged to *S. mamillatum*. However, despite an extensive search we found no other flowering *Syzygium* species within our study area during the time of mist-netting. Only a few pollen grains from other plant families were found in the samples, which suggested that birds visited mainly *S. mamillatum*.

In contrast to our prediction, the overall mean visitation rate (*i.e.*, the number of visitors per tree divided by the number of flowers observed) was lower in the CMA than in the unrestored area ($t = –2.65$, $df = 17$, $p = 0.017$; Fig. 2a). Although mean bout lengths was not statistically different in both habitats ($t = –1.67$, $df = 17$, $p = 0.12$), birds in the unrestored area probed almost twice as many flowers per visit than those in restored areas (Fig. 2b). No significant spatial autocorrelation was found for visitation rate ($r = –0.12$, $p = 0.72$), hence our sampled trees can be considered as statistically independent within-site replicates. Trees with many flowers attracted more birds than trees with fewer flowers ($r = 0.48$, $n = 19$, $p = 0.036$), and birds that visited trees with many flowers probed, on average, more flowers than those on trees with fewer flowers ($r = 0.59$, $n = 19$, $p = 0.004$). Visitation rate of the grey white-eye

was higher in the unrestored area than in the CMA although the total number of grey white-eyes observed was twice as high in the CMA (Table 1). There was no significant difference in visitation rate of red-whiskered bulbuls between sites. The grey white-eye, despite being the most abundant flower visitor, carried significantly fewer *Syzygium* pollen grains than the red-whiskered bulbul, the second most abundant visitor (Table 1).

Plant morphometrics and reproductive performance

Trees in the CMA and the unrestored area were of similar height ($F_{1,110} = 0.02$, $p = 0.90$), although trees inside the CMA had a larger diameter at breast height (dbh; 6.5 ± 0.19 cm) than trees in the unrestored area (5.6 ± 0.18 cm; $F_{1,116} = 4.58$, $p = 0.035$). We found a positive relationship between dbh and the number of buds per tree ($r = 0.37$, $n = 118$, $p < 0.001$), indicating that bigger trees were more abundant in the CMA and produced more buds.

Several trees in the CMA produced a high number of buds (14.6% > 2000 buds; 691 ± 1295 SD) in contrast to trees in the unrestored area (3.1% > 2000 buds; 338 ± 597 SD). However, we found no statistically significant differences in mean number of buds and flowers per tree between the two areas presumably due to a greater variance in the CMA (Fig. 3a). Similarly, mean fruit production per tree was not significantly higher in the CMA than in the unrestored area (Fig. 3b). Since the majority of *S. mamillatum* trees grow in the CMA, we recorded an overall 4.5-fold difference in total number of fruits (8343 vs. 1816) and a 3.5-fold difference in the total number of seeds (18,772 vs. 4907) between the CMA and the unrestored area. During the second fruit count in February 2004, we counted a total of 2744 fruits in the restored and 974 fruits in the unrestored site. The number of fruits per tree was not related to the proportion of fruits lost (only trees with > 10 fruits; $F_{1,63} = 0.93$, $p = 0.34$), and the latter did not differ between sites ($F_{1,63} = 1.39$, $p = 0.24$).

Average fruit set per tree was lower in the CMA than in the unrestored area (overall fruit set: 0.248 ± 0.019), and mean number of seeds per fruit (overall 2.14 ± 0.39) showed a trend ($p = 0.057$) towards fewer seeds per fruit in the CMA (Fig. 3c). Neither fruit nor seed set data were spatially autocorrelated (fruits: $r = –0.05$, $p = 0.92$; seeds: $r = 0.03$, $p = 0.26$). Fruit set increased significantly with increasing visitation rate ($r = 0.53$, $n = 19$, $p = 0.020$). Fruit set and the number of seeds per fruit could not be sufficiently explained by management scheme, ‘mean number of flowers’ per tree and ‘visitation rate’ (fruit set: adj. $R^2 = 0.23$, $F_{3,14} = 2.68$, $p = 0.087$) or nearest neighbor distance, respectively (seeds/fruit: adj. $R^2 = 0.05$, $F_{3,51} = 1.86$, $p = 0.15$).

Mean fruit size per tree in the CMA was 17.4 ± 0.32 mm, while it was larger in the unrestored areas, measuring 18.4 ± 0.33 mm ($F_{1,53} = 4.57$, $p = 0.037$). Although there was a strong positive correlation between fruit size and weight ($r = 0.86$, $p < 0.001$), we found no significant difference in fruit weight between sites (restored: 5.60 ± 0.28 g; unrestored: 6.25 ± 0.33 g; $F_{1,53} = 2.18$, $p = 0.146$). Interestingly, 73% of fruits overall developed at a height of less than 30 cm on the trunk.

DISCUSSION

Herbivory limits fruit production

A substantial proportion (48%) of *S. mamillatum* buds was destroyed by *Polyhymno* larvae, which resulted in a considerable reduction of the reproductive output of *S. mamillatum*. Little is known about the genus *Polyhymno* and host–plant records for only six *Polyhymno* species exist for Leguminosae in the Nearctic, India and the African tropics (Robinson *et al.* 2001). The rate of destruction was higher inside the CMA than outside (~61% vs. ~28%), which may be explained by lepidopteran herbivores relying primarily on visual and olfactory cues for host–plant selection (Finch & Collier 2000). Host trees in the CMA may simply be more visible or smell more conspicuously than host trees in the unrestored area, which are obscured by the dense undergrowth (Wiklund 1984, Chew & Courtney 1991). A trade-off between maximizing floral display to attract pollinators and minimizing visibility to herbivores has been stressed by other authors (e.g. Fenner *et al.* 2002, Juenger *et al.* 2005) and may play a role in our system. The positive correlation between the attack rates and number of buds per tree suggests positive density-dependence. The impact of herbivorous larvae on the reproduction of endangered endemic trees in Mauritius warrants further research because their impact on potential seed set can be substantial.

Pollination biology

The endemic grey white-eye was the most abundant visitor to *S. mamillatum* flowers, followed by the endemic Mauritius bulbul and the introduced red-whiskered bulbul. Bird pollination of *S. mamillatum* contrasts with the typical pollination biology of the Myrtaceae, described as a generalized pollination system with a wide range of vertebrate and invertebrate floral visitors (Hopper 1980, Lack & Kevan 1984, Hingston *et al.* 2004, Boulter *et al.* 2005). Nocturnal flower visitors, such as hawkmoths, cannot be excluded with certainty, but their contribution to pollination is likely to be minimal because flowers opened early in the morning and anthesis lasted for one day only.

Total fruit and seed production and pollinator abundance were greater in the restored area. However, visitation rate (i.e. number of visits per flower) was higher in the unrestored area, resulting in higher fruit set and a trend towards more seeds per fruit, and fruits were larger but not heavier in the unrestored area. Thus, why do trees, with respect to pollination, appear to perform better in the unrestored area? Gross fruit and seed production is largely dependent on the number of trees in each area. There are two possible explanations for the discrepancy in visitation rates and fruit-to-flower ratios between sites.

First, avian foraging behavior may differ with habitat structure. Trees surrounded by dense undergrowth may offer higher protection from predators, resulting in longer stays and potentially greater pollen transfer in such patches. Bird visitation behavior may also explain differences in seed set. We showed a positive correlation between floral abundance and bout length, which could have resulted in a higher proportion of intra-tree pollen transfer in the CMA and consequently in lower seed set due to self-incompatibility. Klinkhamer and de Jong (1993) proposed that optimal plant fitness is obtained by displaying an intermediate number of flowers. Trees in the restored area which bear many flowers may therefore experience more self-pollination, resulting in lower fruit set and number of seeds per fruit than trees in the unrestored habitat, where floral abundance was low. Proença and Gibbs (1994) described late-acting self-incompatibility for several Brazilian Myrtaceae species, which might also be the case for *S. mamillatum*. Our study showed that the flower-to-fruit ratio in *S. mamillatum* decreased between December 2003 and February 2004, particularly in the restored site (see also Nic Lughadha 1998).

Second, hermaphroditic flowering plants often produce an initial excess of flowers that does not contribute to female fitness through fruit or seed production (Sutherland 1987). Several different mechanisms have been proposed to explain how floral excess production elevates female fitness (Burd 1998). Larger floral displays may attract more pollinators, (Willson & Rathcke 1974, Conner & Rush 1996), may allow higher fruit set in resource-rich years and thereby increase lifetime fitness (Lloyd 1980), or may provide a 'reproductive assurance' against losses to, for example, herbivores or fungi (Ehrlén 1991, Hingston & Potts 2005). Another female function mechanism is selective abortion of fruits. Floral overproduction provides a larger pool from which higher quality fruits can be selectively matured (Janzen 1977, Stephenson 1981), provided there is variation in quality, such as in number of seeds per fruit (e.g. Waser *et al.* 1995) or paternity patterns (Janzen 1974, Charnov 1979, Niesenbaum 1999). In *S. mamillatum* trees in the restored area, these mechanisms may act in concert or individually. Overproduction and fruit maturation is likely to be dependent

on these effects and they appear to be stronger in the restored area. It is unclear what proportion of fruit loss can be ascribed to fruit abortion and how much is due to other causes, such as predation. However, we observed no signs of predation (bite marks of rats or signs of seed predators) on unripe and ripe fruits either on the trunk or the ground.

To summarize, subtle changes in bird behavior through habitat structure could explain higher reproductive performance of trees in the unrestored area. It is, however, encouraging that fruit and seed production in the CMA is high, which is the first requirement for habitat restoration to be successful. Even if the unrestored, relatively dense area may be better for pollinators, it is likely that high competition for nutrients and light has a negative effect on seedling recruitment and reproductive success is actually higher in the restored area.

Pollinator identity

Since specialized nectar-feeding birds are locally extinct in Brise Fér, the pollination service to *S. mamillatum* in Brise Fér must be fulfilled by generalist extant native and introduced bird species. The Mauritius fody *Foudia rubra* (Gmelin) and the olive white-eye *Z. chloronothos* Viellot may have acted as efficient pollinators of *S. mamillatum* in the past. Beak morphology and foraging behavior of grey white-eyes prompt us to suggest that it is not the most efficient pollinator of *S. mamillatum*. Despite having a shorter beak and, therefore, having to probe flowers of *S. mamillatum* more deeply to obtain nectar, the grey white-eye carried only half as many pollen grains as the red-whiskered bulbul. Both species are generalist feeders, but their foraging behaviors differ. After visiting several flowers on one tree, the grey white-eye was often seen to perch and clean its beak vigorously, which may reduce pollen load. In contrast, when the red-whiskered bulbul forages for nectar, the prominent feather-crest often touches the anthers. Therefore, the red-whiskered bulbul is most likely the more efficient pollinator of *S. mamillatum*, but its role as a major seed disperser of invasive plant species may hamper habitat restoration (Linnebjerg 2006). The large amount of *S. mamillatum* pollen found on the mist-netted Madagascar fody individual is intriguing: owing to its short beak, this species must probe the flowers deeply to reach the nectar at the bottom.

Plant recruitment

Successful and sustainable reproduction of plant populations depends firstly on intact plant–pollinator interactions and subsequently on seed-dispersal and seedling recruitment. Physiological and evolutionary theories have been proposed to explain the occurrence of cauliflory and caulicarpy (fruits on the trunk) (Haberlandt 1893, cited in Richards 1996), but

few studies have focused on their ecological significance. It may be that caulicarpy, rather than being seen simply as an inevitable consequence of cauliflory, is the more significant trait with respect to selective forces acting on the reproductive display of *S. mamillatum* (see also van der Pijl 1957). As a result, this peculiar flower presentation low on the stem may occur primarily to ease access for ground-dwelling seed dispersers to the fruits (Hopper 1980, Beardsell *et al.* 1993, Warren *et al.* 1997, Kaiser 2006).

Implications for Conservation

Although the degradation of the native Mauritian flora and the subsequent restoration programs have been well described (Vaughan & Wiehe 1941, Page & d'Argent 1997, Mauremootoo *et al.* in press-b), little is known about the rate of regeneration in CMAs and, therefore, the 'success' of these management strategies.

Prior to our study, Brise Fér CMA was thought to contain one of the last populations of the rare endemic tree *S. mamillatum* comprising no more than 20 individuals (J.-C. Sevathian, pers. comm.). In our survey in Brise Fér we found 119 mature individuals, all of which have been marked and mapped and, therefore, can be closely monitored in the future. Our finding that trees in unrestored areas perform slightly better overall, presumably due to the denser understorey, indicates that the current management strategy – at least in the short term – may be missing a crucial factor. Paradoxically, the restoration process of weeding exotic plants creates a disturbance that may affect the behavior of invertebrate pest insects and bird pollinators. As a practical recommendation, we suggest that weeding in CMAs should be conducted with a minimum of disturbance and perhaps as a temporally more gradual removal of exotic plants, which would promote structural habitat heterogeneity (see Hobbs & Huenneke 1992, D'Antonio & Meyerson 2002).

In conclusion, for the management of rare declining species it is important to consider mutualistic and antagonistic interactions and to accept that these interactions may be provided by exotic and/or generalist species since formerly widespread specialists or generalists are now locally extinct. Our study highlights the futility in reconstructing original habitat conditions without incorporating information on ecosystem functions. On tropical oceanic islands, little is known about the original network of interactions among native plant and animal species. Although it will be impossible to consider the full community background, restoration should focus at least on the functionally most important interactions and on

structural habitat traits, taking steps towards a broader understanding of ecosystem functioning.

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Table 1 Visitation rate and pollen load of four different species of birds visiting *Syzygium mamillatum* in the restored and the unrestored area. Ten trees in each area were observed for a total of 30 h. Visitation rate is defined as the number of visitors divided by the total number of flowers observed per hour. One bird species *F. madagascariensis* was not observed visiting our trees but caught in the mistnet. Pollen swabs revealed that this species was carrying pollen of *S. mamillatum.* Pollen load is given as mean ± SE number of pollen grains and N refers to the number of birds captured by mist nets. Annotations show pairs for analysis. E = endemic; I = introduced.

			Restored			Unrestored				
Visitor species	Common name	Status	No. of individuals observed	No. of flowers probed	Visitation rate	No. of individuals observed	No. of flowers probed	Visitation rate	Pollen load	*n*
Zosterops mauritianus	Grey white-eye	E	52	518	0.032[a]	25	188	0.22[a]	949 ± 422[c]	16
Pycnontus jocosus	Red-whiskered bulbul	I	5	93	0.0005[b]	4	16	0.01[b]	2357 ± 761[c]	7
Hypsipetes olivaceus	Mauritius bulbul	E	3	83	n/a	0	0	n/a	272	1
Foudia madagascariensis	Madagascar fody	I	0	0	n/a	0	0	n/a	8308	1

[a] Student's t-test $t = -2.57$, $df = 17$, $p = 0.020$
[b] Student's t-test $t = -0.81$, $df = 17$, $p = 0.43$
[c] Wilcoxon-Mann-Whitney $U = 23.0$, $n = 22$, $p = 0.027$

FIGURES

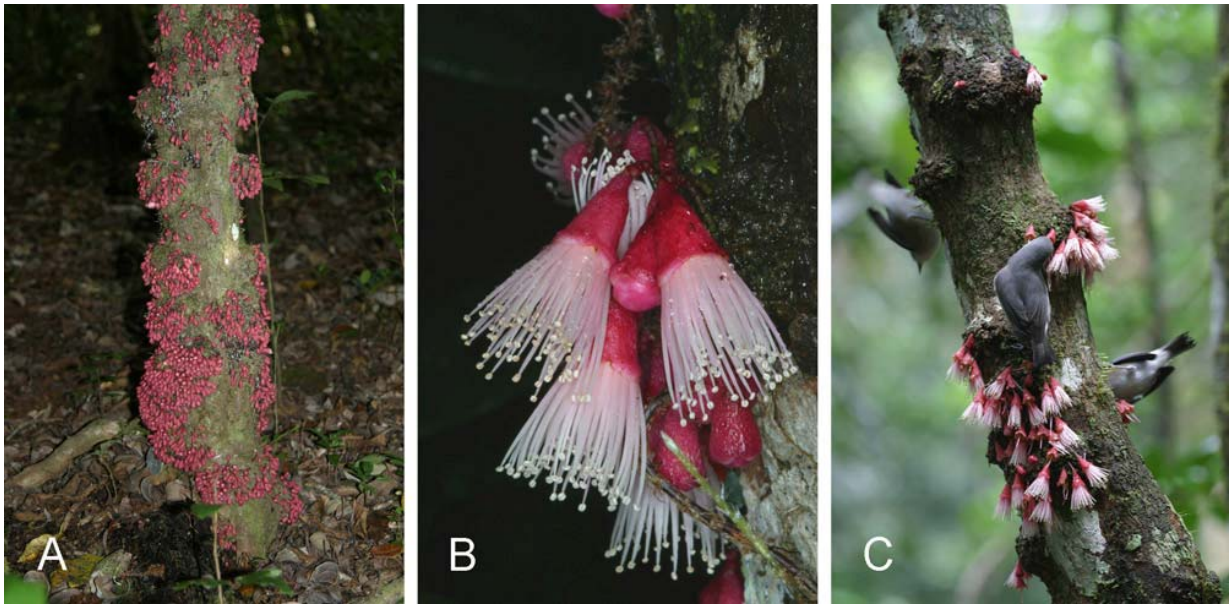


Figure 1 Floral characteristics of *Syzygium mamillatum*. (A) Buds are displayed on burrs along the stem, mainly at the base of the trunk. (B) Open flowers of *S. mamillatum* were visited by (C) Grey white-eyes foraging for nectar.

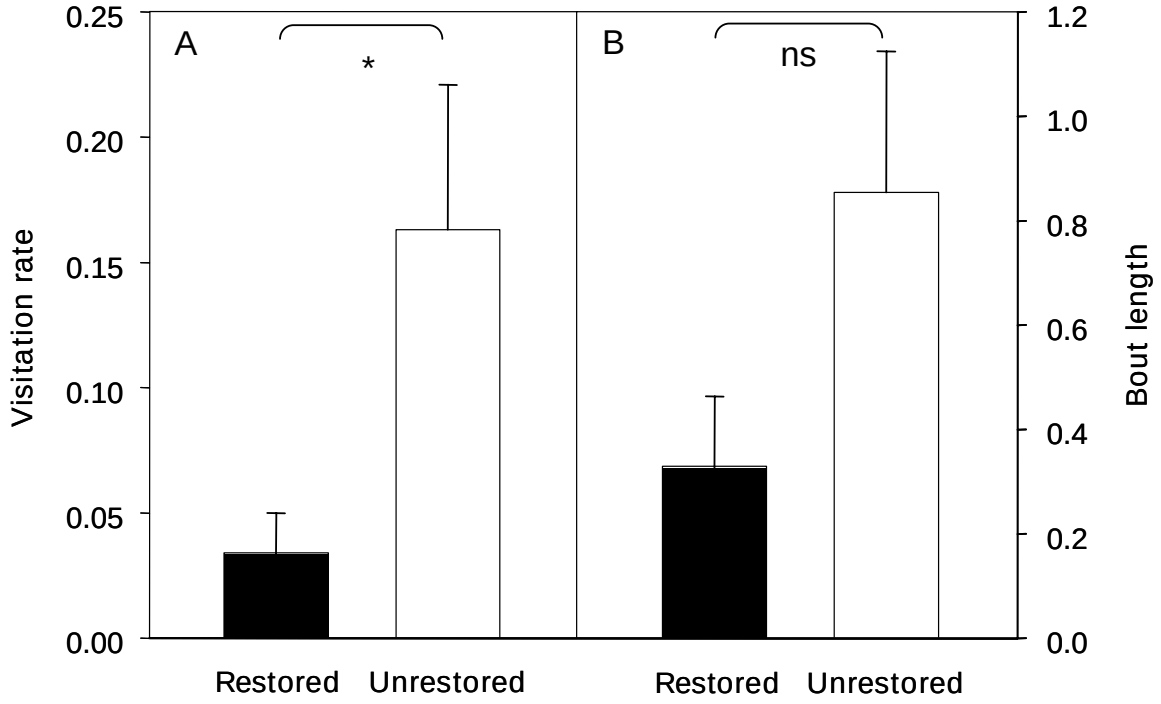
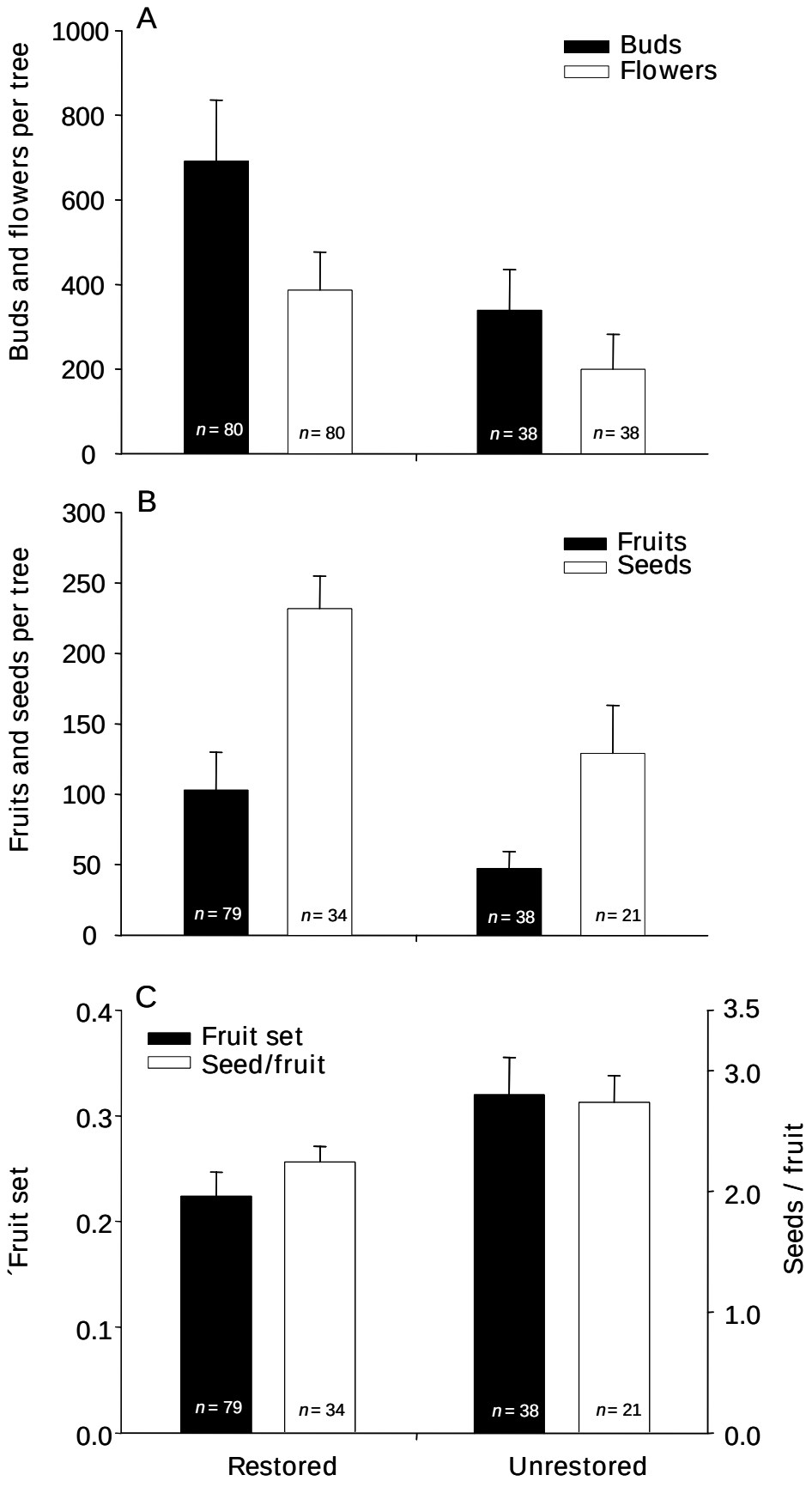


Figure 2 Differences in mean (+ SE) (A) visitation rate and (B) bout length per tree in restored (n = 9 trees) and unrestored areas (n = 10 trees). *, $p < 0.05$; ns, not significant. Visitation rate is the number of birds visiting during one observation unit (= per tree) divided by the number of observed flowers. Bout length refers to the number of probed flowers per tree per observation unit divided by the number of observed flowers.

Figure 3 (next page) Differences in mean (+ SE) (A) number of buds (initial) and flowers (after herbivore attack) per tree, (B) number of fruits and total number of seeds/fruit per tree, and (C) fruit set and number of seeds/fruit per tree in restored and unrestored areas. Fruit set is defined as number of fruits divided by number of flowers per tree. Total number of seeds per fruit was calculated for each tree based either on mean seeds/fruit from individual counts of trees or from the overall mean. In (A) both number of buds and flowers per tree were not significantly different between management schemes (buds: $t = –1.21$, $df = 117$, $p = 0.23$; flowers: $t = –0.18$, $df = 117$, $p = 0.86$). (B) Number of fruits ($t = 0.58$, $df = 115$, $p = 0.57$) and seed/fruit per tree ($t = 1.18$, $df = 115$, $p = 0.24$) were not different between sites. In (C) fruit set was significantly different between sites ($t = –2.72$, $df = 115$, $p = 0.007$) and number of seeds per fruit per tree showed a trend towards more seeds in fruits from the unrestored area than fruits from the CMA ($t = –1.95$, $df = 53$, $p = 0.056$). For the analysis of number of seeds per fruits, fruits were collected from 55 trees in total.


A
Buds
Flowers
Buds and flowers per tree
1000
800
600
400
200
0
n = 80
n = 80
n = 38
n = 38
B
Fruits
Seeds
Fruits and seeds per tree
300
250
200
150
100
50
0
n = 79
n = 34
n = 38
n = 21
C
Fruit set
Seed/fruit
´Fruit set
Seeds / fruit
0.4
0.3
0.2
0.1
0.0
3.5
3.0
2.0
1.0
0.0
n = 79
n = 34
n = 38
n = 21
Restored
Unrestored

CHAPTER 3

Endangered endemic plants on tropical oceanic islands: seed dispersal, seedling establishment, and ecological analogues

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ABSTRACT

The Janzen-Connell model states that host-specific seed predators, or seedling herbivores and pathogens may have a disproportionately large negative effect on progeny close to maternal trees. The vast majority of both experimental and theoretical studies addressing the Janzen-Connell model have explored how it can explain existing patterns of species diversity in tropical mainland areas. We investigated the validity of the predictions of the Janzen-Connell model on oceanic islands in a conservation context, by experimentally studying seed germination and seedling survival patterns of the critically endangered endemic Mauritian plant *Syzygium mamillatum* (Myrtaceae) in relation to proximity to maternal trees. We also experimentally evaluated the use of ecological analogue animals to resurrect the functional component of extinct frugivores. Seed germination patterns were strongly affected by propagule type (whole fruits, depulped seeds, and gut-passed seeds), but there was no effect of proximity to maternal tree on germination patterns. Contrary to this, we found strong negative effects of proximity to maternal tree on seedlings, thus providing the first experimental evidence of a distance-dependent Janzen-Connell effect from an oceanic island. Seedlings close to maternal trees had fewer leaves, suffered more damage from natural enemies, and survived less well compared to seedlings away from maternal trees. We successfully used giant Aldabran tortoises as ecological analogues for extinct Mauritian frugivores. Effects of gut-passage were negative at the seed germination stage, but seedlings from gut-passed seeds grew taller, had more leaves, and suffered less damage from natural enemies than any of the other seedlings. We discuss how ecological analogue species may be used to replace extinct frugivores in oceanic island ecosystems.

INTRODUCTION

Animal-mediated seed dispersal and subsequent differences in seedling establishment and survival in relation to distance from adult conspecific plants are important factors in the dynamics of tropical forests (Harms *et al.* 2000, Howe & Miriti 2000). This has been intensely studied during the last three decades in the framework of the Janzen-Connell model (Janzen 1970, Connell 1971, Clark & Clark 1984), which states that host-specific seed predators, or seedling herbivores and pathogens may have a disproportionately large negative effect on progeny close to maternal trees. Hence, a major positive effect of seed dispersal away from maternal trees is that seeds and seedlings may escape from adverse pressures by natural enemies into a more benign neighbourhood for establishment and survival (Howe & Smallwood 1982). However, the vast majority of both experimental and theoretical studies addressing the Janzen-Connell model have been primarily concerned with exploring how it can explain existing patterns of species diversity and were less concerned with the potential importance of this pattern for conservation ecology (reviewed in e.g. Wright 2002).

The Janzen-Connell model on oceanic islands

Many studies have investigated mechanistic aspects of seed dispersal interactions on oceanic islands (e.g. seed rain, effects of gut-passage on seed germination, and seedling survival). However, few studies have investigated aspects of seed dispersal and seed- and seedling survival in the framework of the the Janzen-Connell model on oceanic islands. Clark and Clark (1981) showed that, while most seeds of *Bursera graveolens* (Burseraceae) in the Galápagos Islands were found directly beneath the maternal plants, most saplings were found away from conspecific adults. In another study on a small atoll in the Pacific Ocean, Lee (1985) described a similar pattern for *Pandanus tectorius* (Pandanaceae), whose main disperser is the land crab *Cardisoma carnifex*. For the critically endangered tree *Serianthes nelsonii* (Fabaceae) in the Mariana Islands, there is no seed dispersal away from maternal trees, and the few seedlings that germinate beneath the maternal trees do not survive (Wiles *et al.* 1996). Lastly, in a laurel forest on the Canary Islands, Arevalo and Fernandez-Palacios (2003) investigated the spatial distribution of saplings of several tree species. They found no effect of distance to conspecific adults on sapling density, suggesting that Janzen-Connell spacing plays a minor role in this forest.

However, despite a long scientific history of using islands as natural laboratories for ecological and evolutionary studies (e.g. Vitousek *et al.* 1995, Grant 1998), we are not aware of any studies that have experimentally investigated seed germination and the fate of post-

germination seedlings in the framework of the Janzen-Connell model on oceanic islands. Consequently, while it is acknowledged that oceanic islands harbour many of the most critically endangered plant species in the world, we know next to nothing about how one of the most widely studied ecological patterns affects the regeneration and longer-term survival of these plants.

Two key points emerge in relation to the Janzen-Connell model and how it applies to oceanic island ecosystems. Firstly, patterns of seed- and seedling mortality on islands may be different from those found in mainland ecosystems. Generally, a high host-specificity of herbivores and pathogens is an assumption of the Janzen-Connell model (Clark & Clark 1984). Island ecosystems are often simpler than mainland ecosystems, in which case we would expect more generalist than specialist seed predators and herbivores than on the mainland. If so, we could expect Janzen-Connell patterns to be less prevalent on oceanic islands than in comparable mainland habitats. There have been many studies on specialist versus generalist herbivorous insects in tropical forests (reviewed in Novotny & Basset 2005), but very little is known about the relative importance of specialist and generalist insect herbivores on oceanic islands (Ribeiro *et al.* 2005). The second key point is that studies of Janzen-Connell patterns are more urgent for oceanic islands than for most mainland ecosystems. Pristine oceanic islands typically harbour fewer species of frugivorous vertebrates than comparable mainland areas, and many of those few species are now extinct (Cox *et al.* 1991). Thus, there are currently many oceanic islands where the frugivorous members of the afterlife (*sensu* Lawton 1995) outnumber the living, and many seed dispersal interactions are likely to have been lost. Today, the remaining native and endemic flora and fauna of many oceanic islands are often crammed into much smaller remnant patches of native habitats than those on the mainland. Therefore, if Janzen-Connell patterns are indeed prominent on oceanic islands, endangered plant species once relying on vertebrate dispersal by now-extinct animals face a double peril: not only do they lack most of the agents that once mediated the escape and establishment of their progeny away from maternal trees, but present-day areas with native habitats may be too small to support viable populations of plants that exhibit strong Janzen-Connell spacing patterns as a result of natural enemies.

Ecological analogue species and the resurrection of extinct interactions

One way of recreating some of the lost seed dispersal dynamics in native habitats is to introduce species that are ecologically analogous to extinct ones. That is, using extant, seed-dispersing animals to perform the same or similar ecological functions as the extinct species.

To some ecologists and conservation biologists this idea may be anathema; in a best-case scenario it could be seen as little more than an attempt to create a small-scale version of Jurassic Park, and in one worst-case scenario it runs the risk of introducing species that may become invasive and have unintended negative effects on the ecosystem. Recently, the use of ecological analogue species to recreate the Pleistocene megafauna in the USA and the Siberian Tundra has been the subject of a heated debate (Dinerstein & Irvin 2005, Donlan 2005, Smith 2005, Zimov 2005), partly due to the complexity of the involved ecosystems, and partly because of the vast areas needed to sustain populations of the suggested large-bodied animals. In contrast, due to their relatively small size and relative simplicity of their native ecosystems, oceanic islands may be ideal systems in which to empirically explore the use of ecological analogue species in a conservation management context (Jones 2002, Steadman & Martin 2003).

Our study

Here, within the framework of the Janzen-Connell model, we experimentally investigate seedling establishment and survival of a critically endangered tree species on the oceanic island of Mauritius. Furthermore, we assess the use of ecological analogue seed-dispersing species to resurrect the functional component of extinct endemic frugivores.

We used the oceanic island of Mauritius as our model system because it faces most of the problems that affect oceanic island ecosystems in general. Mauritius has lost the majority of its original vertebrate frugivorous and seed dispersing fauna, and some studies have suggested that missing seed dispersers could be contributing to the continued decline in many of the endangered Mauritian plant species (Vaughan & Wiehe 1941, Maunder *et al.* 2002, Cheke & Hume in press). There are many Mauritian plants with fleshy fruits, and a number of early observations of the now extinct frugivores feeding on these (see Cheke 1987, Cheke & Hume in press). Despite this, very few studies have directly addressed the role of extant or extinct seed dispersal interactions in forest dynamics in present-day Mauritius (but see Nyhagen *et al.* 2005).

We used the critically endangered endemic plant *Syzygium mamillatum* (Myrtaceae) as our model organism to study the effect of missing seed dispersers in the dynamics of present day native forests in Mauritius. The majority of experimental studies investigating the Janzen-Connell model have tested it at the seed level (Hyatt *et al.* 2003). However, this may not be the best stage in the reproductive cycle, as predators of seeds in general may be more generalised than herbivores or other predators at the seedling level (Janzen 1971).

Furthermore, in any given year, most seeds will be destroyed regardless of distance to maternal tree; hence, distance-related differences in mortality should be more marked for seedlings than for seeds (Connell 1971).

We focused on seed germination, and the establishment and survival of seedlings of *S. mamillatum*. We addressed the specific questions: Are seed germination, and seedling growth and survival of *S. mamillatum* affected by distance to maternal trees? If so, can we use extant frugivorous animals as ecological analogue species to resurrect lost forest dynamics and ameliorate the negative effects?

MATERIAL AND METHODS

Study site

The study was conducted in the Black River Gorges National Park in Mauritius between March 2004 and February 2006. The study site was a 24 ha fenced and weeded Conservation Management Area (CMA) that was established in the upland forest of Brise Fér in 1996 (20°22.5'S, 57°26'E, 570–600 m elevation). Outside the CMA, the native forest is heavily degraded by invasive species, mainly strawberry guava *Psidium cattleianum*, privet *Ligustrum robustum* and the weedy *Clidemia hirta*. A detailed description of the vegetation in Brise Fér is given in Lorence & Sussman (1986). Annual rainfall is 2400 mm, annual mean temperature is around 20°C, and the forest is classified as a lower montane evergreen wet forest (Vaughan & Wiehe 1941, Lorence & Sussman 1986). The Brise Fér forest lies on a relatively narrow plateau, approximately 1500 × 500 m in size, with the CMA located in the central eastern part (Fig. 1). Within the CMA, the forest is heterogenous. It is roughly divided by a steep slope of 15–25 m in height into an upper southwestern plateau, characterised by a thin layer of top soil (erosion area), and a lower northern and northeastern plateau with deeper soil (accumulation area; Vaughan & Wiehe 1941). The forest structure reflects this soil difference, with a relatively low forest of a height of 8–12 m on the upper plateau and a taller forest with much larger trees of 15–25 m on the lower plateau. The forest on the upper plateau is more open and dry than the forest on the lower plateau.

Study species

Syzygium mamillatum (Myrtaceae) is a critically endangered endemic sub-canopy tree of the upland Mauritian rainforest, and grows to 2.5–9 m in height. Despite the striking basal cauliflory of *S. mamillatum* (most flowers are on the lowest 1–1.5 m of the trunk), the species was not described until 1987 (Bosser *et al.* 1987). While a few single trees or small stands are

known from elsewhere in the national park (e.g. Macabé, Mare Longue and Mt. Cocotte, pers. obs.), the largest known population is located in Brise Fér. Previous surveys suggested a maximum of 20 *S. mamillatum* trees in this area but, during a focussed search in July and August 2003, we found a total of 119 mature trees – representing the largest known population with 87% of all known mature trees of this species. The majority of trees in this population occur within the CMA (81 trees = 68%). The difference between upper and lower plateau in the CMA was apparent in the size of adult *S. mamillatum* trees. Of the 81 adult trees in the CMA, 79 were upright and the remaining two trees had been partly knocked over by falling trees. Of the upright trees, 58 grew on the lower plateau and 21 on the upper plateau. Trees growing on the lower plateau were larger than trees growing on the upper plateau, in terms of both height (all values are mean ± SD, compared with Student's *t*-tests; lower plateau = 6.2 ± 1.4 m, upper plateau = 5.2 ± 1.3 m, $t = 2.91$, $p = 0.006$) and diameter at breast height (lower plateau = 6.8 ± 2.2 cm, upper plateau = 5.3 ± 1.7 cm, $t = 3.08$, $p = 0.004$).

In our first ecological study of *S. mamillatum* (Chapter 2), we investigated its pollination biology, and found it to be pollinated by endemic as well as introduced bird species. The average fruitset of trees in the CMA was 20–25%, with trees producing 1–520 ripe fruits (mean ± SD: 48 ± 100 fruits; $n = 69$ trees). On average, 73% of all ripe fruits on a tree developed on the lowest 30 cm of the trunk (Chapter 2; Appendix I Plate A). After flower pollination in November–December, fruits take 4–5 months to ripen, and turn pale green or pale pink when ripe. They are 30–50 mm long, 15–30 mm wide at their widest point, and weigh some 4–10 g (Chapter 2; Appendix I Plate B). Depending on ripeness, the pulp has the texture of a soft pear, with a relatively strong fermenting smell. In ripe fruits, the 2–4 seeds are easily separated from the pulp as a coherent entity, forming a rough 'ball' shape (Appendix I Plate C). Individual seeds are green without a hard seed coat, only a layer of wet and semi-fibrous pulpy tissue (Appendix I Plate F). Every seed has a well-defined raphe down the middle, separating the two cotyledons (Appendix I Plate D, F), along which they break quite easily if minimum force is applied. The cotyledons are bright green, and can stay that colour for up to 8–10 months under field conditions (pers. obs.).

We performed our study on *S. mamillatum* inside the CMA only, because the CMA contains the largest remaining population of *S. mamillatum*, and because almost no seedlings of native or endemic plant species survive to sapling stage in the heavily invaded forest outside of the CMAs , due to both competition with invasive plants and grazing/foraging by introduced animals (Lorence & Sussman 1986, Mauritian Wildlife Foundation unpublished database). It is most likely that survival of the native Mauritian forests will depend on

weeding of invasive plant species and control of introduced animal species for the foreseeable future. Therefore, it is of greatest applied and immediate conservation importance to investigate and attempt to re-establish some of the lost dynamics in the remaining native Mauritian forests within the CMAs.

STATISTICAL ANALYSES

Statistical models and methods used are specified in the relevant sections. All analyses were done with R.2.2.1 (R Development Core Team 2005).

Soil analysis

To investigate soil quality on the upper versus the lower plateau, we collected five soil samples from each. To obtain a sample, we walked random transects of ~50 m and took a spoonful of soil every 2–3 m. Soil was brought to Switzerland two days after sampling, and sent for analysis (Labor für Boden- und Umweltanalytik, CH-3602 Thun). The average values for pH, humus, clay, nitrogen, phosphorpus, potassium, calcium and magnesium of soils from the upper and the lower plateau were compared with Wilcoxon-Mann-Whitney tests.

Natural seedling survey

During the search for adult trees in Brise Fér, we only found seedlings around the base of adult trees, no more than 1 m away from the trunk. However, this may have been biased as we were not actively looking for seedlings on the forest floor while searching for adult trees. Therefore, we searched 10 transects on the upper plateau and 10 transects on the lower plateau. The parallel transects were 200–300 m long and oriented east-west, covering an area that included approximately 70–80% of the adult *S. mamillatum* in the CMA. Along each transect, we looked for *S. mamillatum* seedlings and saplings of any size within a 2 m belt transect. Furthermore, throughout the study period we opportunistically searched for seedlings and saplings throughout Brise Fér CMA.

Feeding experiments with ecological analogue species

Out of the multitude of frugivorous seed-dispersing ghosts in the Mauritian fauna (Appendix Table, Cheke 1987, Cheke & Hume in press), we selected to resurrect and investigate the functional component of three of them, the dodo (*Raphus cucullatus*) and the two species of giant tortoises, the high- or saddle-backed tortoise (*Cylindraspis triserrata*) and the domed tortoise (*C. inepta*). As a dodo stand-in, we used three domestic turkeys (*Meleagris*

gallopavo). However, turkeys have a powerful gizzard with grinding stones, like the dodo had (Hachisuka 1953), and no seeds from the 105 *S. mamillatum* fruits we fed to them passed through unharmed; we only found seed fragments of 1–2 mm in size. Therefore, we conclude that turkeys are not suitable analogue seed dispersers for *S. mamillatum*, and we present no further data from this part. As a stand-in for the two extinct giant tortoise species of Mauritius, we used giant Aldabra tortoises (*Aldabrachelys gigantea = Geochelone gigantea*, Austin *et al.* 2003). All of the extinct Mascarene giant tortoise species have been reported to eat fruits and leaves (review in Cheke & Hume in press). Similarly, the Aldabra tortoise also feeds on many kinds of plant material, including fruits, and acts a seed disperser for several plant species (Hnatiuk 1978). While *Aldabrachelys* is probably not a direct sister genus of *Cylindraspis* (Austin & Arnold 2001), *A. gigantea* is certainly the closest extant analogue of the extinct Mauritian species in ecological terms.

For the feeding experiment, we used three giant Aldabra tortoises from La Vanille Crocodile and Tortoise Park, Riviére des Anguilles (La Vanille hereafter), where they are usually part of a herd of some 200 adult tortoises in a large savannah-type enclosure. The three medium-sized tortoises, weighing approximately 70–100 kg each, were separated from the herd and kept in a smaller enclosure, where they were also being fed vegetables and other fruit throughout the feeding experiment. Forty fruits were fed to the three tortoises twice a week during four weeks, beginning on March 10, and finishing on April 5. A total of 320 ripe fruits from seven different *S. mamillatum* trees were fed to the tortoises (mean = 46 fruits/tree, range: 20–132 fruits/tree). *Syzygium mamillatum* fruits were fed whole to the tortoises (Appendix I Plate E). Opening the fruits and counting the seeds would potentially disrupt the layer of tissue keeping the seeds together (see Appendix I Plate C), which could in turn influence the effects of gut passage. Therefore, we estimated that the fruits fed to the tortoises contained a total of 685 seeds based on the average number of seeds per fruit (2.14 seeds; Chapter 2). Tortoise faeces were collected daily in plastic bags at La Vanille from March 11 to May 5. Once a week, we collected the bags from La Vanille and examined the faeces. Whole *S. mamillatum* seeds and seed fragments, which were large enough to be identified as such (Appendix I Plate G) were extracted, counted and weighed.

Germination experiments

We set up two different seed germination experiments in Brise Fér CMA; one in which we used whole fruits and manually depulped seeds, and another where we used tortoise gut-passed seeds from the feeding experiment. Thus, we are able to compare the performance of

not only gut-passed seeds and manually depulped seeds, but also the performance of seeds from whole fruits and manually depulped seeds. Both experiments were established in March 2004.

For the first experiment, with whole fruits and manually depulped seeds, an unbalanced factorial design with four treatments was set up around 20 maternal *S. mamillatum* trees (if not stated otherwise, the replication is always $n = 15$ maternal trees for lower plateau and $n = 5$ maternal trees for upper plateau): (1) site of maternal trees (fixed factor PLATEAU with two levels: 'upper' and 'lower'), (2) distance from maternal tree (fixed factor DISTANCE with two levels: 'close' and 'away'), (3) propagule type (fixed factor PROPAGULE with two levels: 'seed' and 'fruit'), and (4) protection from vertebrate fruit- or seed predators (fixed factor CAGE with two levels: 'cage' and 'no cage'). The 20 maternal trees were used as a random factor in the analyses. This gave a total of 160 groups of seeds or fruits that will be referred to as 'patches'. Around each of the 20 maternal trees, the four close patches were set up 1 m away from the trunk in the four cardinal compass directions. The four away patches were set up in one of two different ways: either 20–25 m away from the maternal tree in the four cardinal directions, or 20–25 m away in a roughly perpendicular line to the tree with at least 6–8 m between patches. None of the away patches were set up closer than 25 m to any other *S. mamillatum* tree. In each of the seed patches we placed 4–7 seeds with the slimy seed coat attached, as this was difficult to remove from seeds without damaging them. The fruit patches consisted of three whole fruits. Both seeds and whole fruits in any one patch were placed directly on the ground in a 10 × 10 cm area. The cages were built with 0.5 × 0.5" wire mesh, 16 ×16 × 8 cm in size, and were fixed close to the ground by 6–8 metal cramps around the base (Appendix I Plate H). Cages were removed when the first seedling in a caged patch was about to touch the wire mesh, as we wanted to avoid any physical interference with seedling growth. This was done in October–December 2004, when almost all seedlings had emerged and seed predation was no longer considered important (see Appendix I Plate I for a typical patch of seedlings)

Seeds from the feeding experiments were also put out in Brise Fér CMA. Whole tortoise gut-passed seeds and several large fragments (half a seed, one cotyledon) were put out once a week in two caged plots ('plot' hereafter refers only to gut-passed seeds or seedlings), one plot on the upper plateau and one on the lower plateau. Plots were placed a minimum of 25 m away from any *S. mamillatum* tree, and a minimum of 15 m away from each other. Each plot consisted of two 15 × 15 cm sections, one with whole seeds and one with seed fragments, spread out evenly. The two sections in each plot were roughly 30–40 cm

apart and were covered with an amount of tortoise dung corresponding to the average tortoise turd size (roughly 6–8 × 10–15 cm), evenly spread out in a *ca*. 1 cm thick layer. Each plot was covered with a wire-mesh cage of roughly 100 × 100 × 20 cm in size. These cages were removed in December 2004. Two plots were set up each of the first four weeks and four plots were set up in the fifth week, where most seeds were collected. Thus, we had a total of 12 replicates, with $n = 6$ on the upper and $n = 6$ on the lower plateau.

Initial seed numbers in patches

As we put out whole fruits in the fruit patches we did not know how many seeds each fruit contained. Thus, we established a baseline number of seeds for each of these patches for use in subsequent analysis of germination patterns and germination success. This was done by scoring the number of whole seeds as soon as the pulp had decomposed, usually after 1–2 months. We investigated effects of PROPAGULE, DISTANCE, and CAGE on initial numbers of seeds per patch with an ANOVA.

Germination patterns

Seedling germination in patches and plots was recorded six times; roughly once per month for the first four months (where the majority of seeds germinated), and thereafter at different intervals, depending on timing of fieldwork in Mauritius. Germination was defined as the emergence of the first two leaves and not only the root growing into the soil, because many seeds never managed to get past the latter stage, but died before extending the shoot.

Due to the different number of maternal trees on the upper and lower plateau, the loss of several patches to feral pigs that broke into the CMA and to weeders working in the CMA, our experimental design was unbalanced. Furthermore, for the calculation and analyses of proportions of seeds germinated we needed to take the number of initial seeds in each patch into account. We therefore analysed seedling germination patterns with a generalised linear mixed-effects model with penalised quasi-likelihood (hereafter GLMM) (glmmPQL function in R.2.2.1, using the MASS library; Breslow & Clayton 1993; Venables & Ripley 2002), with PLATEAU, DISTANCE, PROPAGULE, CAGE and Time as fixed effects, maternal tree as a random effect, and using a binomial error structure. This method is robust for unbalanced data and by using the ‘cbind’ command to calculate the germination proportions we weighted the sample sizes (number of seeds and seedlings per patch). Initially, we fitted a full model, whereupon non-significant higher-order interactions were removed and only the simplified model is presented.

Overall germination success

The overall germination success (proportion of initial seeds that germinated) was analysed by comparing the proportions of maximum number of seedlings out of the initial number of seeds in each patch with a GLMM, using the same fixed (except for Time) and random effects and error structure as above (for almost all patches the maximum number of seedlings was reached around December–January 2004). Initially, we fitted a full model, whereupon non-significant higher-order interactions were removed to simplify the model.

We compared germination success for gut-passed seeds to manually depulped seeds germinating in cages away from maternal trees only ('away seed cage' patches), using a GLM with a quasi-binomial error structure to account for over-dispersed data.

Seedling morphometrics

We measured the height (from ground to where the uppermost leaf pair was attached to stem) and counted the leaves of all seedlings in each patch and plot twice; once in January 2005 and again in February 2006. For the analysis of the seedlings in patches we used linear mixed-effects models with patch nested in maternal tree as random factors.

For seedling height in the plots we compared average seedling height per plot with height of seedlings in all patches (there was no significant difference in height between patches, see Results), averaged at the maternal tree level, with a Wilcoxon-Mann-Whitney test. Numbers of leaves per seedling in the plots was compared to numbers of leaves per seedling in away patches only, averaged at the maternal tree level, with a Wilcoxon-Mann-Whitney test. For both analyses, we pooled upper and lower plateau maternal trees and plots, as there were only few plots with seedlings germinating.

Seedling damage

We here define seedling damage broadly as a visible mark caused by anything that damages and/or feeds on the leaves. Levels of seedling damage were scored twice, in both patches and plots.

First survey

In the first survey in early January 2005, we randomly selected one seedling from each of the 160 patches where one or more seedlings had emerged and were still alive at this time (n = 117 patches). Due to the low number of emerged seedlings in the plots with gut-passed seeds, we here scored seedling damage on all seedlings and used plot averages in the analysis. We

measured seedling height and counted the number of leaves for each seedling. We assessed the presence or absence of different categories of damage on each leaf, divided into seven categories: 1) leaf mines, 2) necrosis spots, 3) bite damage, 4) discolouration/wilting, 5) curled leaves, 6) fungus, and 7) scale insects. We analysed the proportion of total number of leaves affected by each of the damage categories, as well as the overall proportion of total number of leaves affected by one or more damage categories. We also investigated the diversity of damage categories suffered at the seedling level by analysing the proportion of all seven damage categories present at the seedling level. To weight these proportions in relation to total number of leaves per seedlings, we used GLMMs with DISTANCE and PLATEAU as fixed effects and maternal tree as random effect, and with binomial error structures. A separate model was fitted for each of the seven damage categories, as well as one for overall proportion of damaged leaves and one for diversity of damage at the seedling level. We investigated possible interdependencies between damage categories with Pearson's correlation tests.

Seedling damage in the plots with seedlings from gut-passed seeds was compared to that of away seedling patches, using GLMMs, combining maternal tree and plot into one random effect. Here, we also fitted a separate model for each of the seven damage categories, one for overall proportion of damaged leaves, and one for diversity of damage at the seedling level.

Second survey

In the second seedling damage survey in mid-February 2005, we visually assessed the overall level of damage for all seedlings in each patch and each plot (n = 117 patches and 7 plots), using the following grouping: low (almost no damage, most to all seedlings healthy, only few leaves damaged), medium (little damage, most seedlings healthy with few leaves damaged, one to a few seedlings damaged) and heavy (damage affecting most seedlings, leaves curled or wilting, one to more seedlings badly affected). For statistical analyses, damage levels were assigned a numerical value: low = 1, medium = 2, and heavy = 3. For patches, the results of the second survey were analysed with a linear mixed-effects model (Pinheiro & Bates 2000), using DISTANCE and PLATEAU as fixed effects and maternal tree as random effect.

Seedling damage levels in the plots with seedlings from gut-passed seeds were compared to away patches, averaged at the maternal tree level, with a Student's t-test.

Seedling survival

Seedling survival was investigated by analysing the proportion of surviving seedlings in February 2006 in relation to the maximum number of seedlings in patches where at least one seedling had germinated (n = 132 patches). We used a GLMM with a binomial error structure. We initially fitted a full model with all factors (fixed: PLATEAU, DISTANCE, PROPAGULE, CAGE; random: maternal tree). Any significant or marginally significant factors or interactions between factors were retained, and included in a new minimum adequate model.

Again, survival of seedlings in plots was compared to survival of away seedling patches only. We used a GLMM for the analysis, combining maternal tree and plot into one random effect.

RESULTS

Soil analysis

There were a few significant differences in soil properties between the upper and the lower plateau: There was more clay on the lower plateau (all means ± 1 SE; upper: 11.0 ± 0.0%, lower: 16.0 ± 1.6%; W = 2.5, p = 0.023), and a higher humus content on the upper plateau, but in absolute numbers the difference was small (upper: 4.1 ± 0.1%, lower: 3.6 ± 0.1%; W = 23.0, p = 0.021). The only significant difference in soil nutrients or minerals was found for potassium (upper: 55.0 ± 6.3 mg/kg, lower: 90.0 ± 6.9 mg/kg; W = 2.0, p = 0.032), while comparisons of all other soil properties were non-significant.

Natural seedling survey

We found no natural *S. mamillatum* seedlings or saplings away from maternal trees on any of the transects. Natural seedlings were usually confined to a distance < 1 m away from the trunk of maternal trees; the only exception being for a few trees growing on slopes, where some seedlings were found up to 2–3 m downhill. We found the tallest natural seedlings (30–40 cm) around the three adult trees in the Old Plot (see Fig. 1), which has been weeded since 1987. However, these were all in a bad shape with only a handful of heavily damaged leaves left. There were also several wilted and dead seedlings of the same size.

Feeding experiments with ecological analogue species

Of the estimated total of 685 seeds fed to the giant tortoises, 108 (15.8%) passed unharmed, and we recovered an additional 419 fragments with a total weight of 143.9 g, corresponding to approximately 197 seeds (28.8%). Thus, an estimated 380 seeds (55.4%) were digested, at

least partly. Minimum gut passage time was 12 days (from first feeding March 10th to first seed defecated March 22nd), with a theoretical maximum of 43 days (from first feeding to last seed defecated April 22nd). Because we fed the giant tortoises continuously over several weeks, to avoid overfeeding them an unusual food item, we cannot calculate a mean gut passage time. However, the temporal distribution patterns of gut-passed seeds and seed fragments in relation to the period of feeding suggests a mean gut passage time of 2–3 weeks (Fig. 2).

Germination experiments

Initial seed numbers in patches

Each patch contained 5–6 seeds when it was set up (mean ± SD = 5.4 ± 1.6 seeds). There was no significant effect of PROPAGULE ($F_{1, 147} = 0.142$, $p = 0.71$) or DISTANCE ($F_{1, 147} = 0.141$, $p = 0.71$) on initial numbers of seeds per patch. However, patches with cages contained on average more seeds than uncaged patches (5.7 ± 1.6 *vs*. 5.1 ± 1.5 seeds; $F_{1, 147} = 4.68$, $p = 0.03$). This difference, though, was only found for FRUIT (cage: 6.0 ± 2.1 seeds, no cage: 4.8 ± 2.0 seeds) and not for SEED (cage: 5.3 ± 0.89 seeds, no cage: 5.4 ± 0.79 seeds; CAGE × PROPAGULE: $F_{1, 147} = 14.23$, $p = 0.02$). This suggests that pre-germination predation in patches is mostly restricted to whole fruits.

Germination patterns

There were no significant main effects of PLATEAU or DISTANCE on the overall germination pattern (Fig 3a, b; Table 1). However, seeds from whole fruits germinated both faster and with a higher proportion than manually depulped seeds (Fig. 3c; Table 1). Germination was faster with cage than without cage (Fig. 3d; Table 1), but only for seeds from whole fruits (Fig.3e; Table 1). Furthermore, there was a significant interaction between PROPAGULE and PLATEAU. While there was no difference in germination pattern for seeds from whole fruits on the upper and lower plateau, manually depulped seeds germinated worse on the upper than on the lower plateau (Fig. 3f; Table 1). However, the germination pattern was not significantly different over time (PROPAGULE × PLATEAU × Time, $p > 0.50$ not included in final model reported in Table 1).

For gut-passed seeds, there were too few plots ($n = 7$ plots) where seeds germinated to perform germination pattern analyses with plot as a random factor. However, when plotting the germination for all gut-passed seeds pooled (Fig. 3c, $n = 108$ seeds), they appeared to

germinate more slowly and at a lower proportion than both manually depulped seeds and seeds from whole fruits.

Overall germination success

At maternal tree level a grand mean of 60.4 ± 0.03% (all means ± 1 SE) of the seeds germinated. In the GLMM, the only significant factor was PROPAGULE, with mean germination rates being 70.9 ± 0.04% for seeds from whole fruits and 49.3 ± 0.05% for manually depulped seeds ($F_{1, 131} = 20.9$, $p < 0.001$). There was a marginally significant interaction between PROPAGULE and PLATEAU ($F_{1, 131} = 2.96$, $p = 0.088$), explained by a difference in germination on upper versus lower plateau for manually depulped seeds (upper: 33.4 ± 0.1%, lower: 54.7 ± 0.1%) but not for seeds from whole fruits (upper: 71.4 ± 0.1%, lower: 70.7 ± 0.1%).

Seeds only germinated in seven of the 12 plots, and germination success of the gut-passed seeds in the plots was significantly lower than the 'away seed cage' patches used as the control (gut-passed seeds: 18.2 ± 7.0%, control: 47.4 ± 7.6%, $F_{1, 29} = 6.24$, $p = 0.018$). There appeared to be a negative effect of mean gut-passage time on germination success, with the first seeds collected germinating better than the last seeds (Fig. 4).

Seedling morphometrics

In 2005, DISTANCE had a highly significant effect on number of leaves per seedling, with more leaves per seedling away (7.6 ± 0.3 leaves) than close (6.2 ± 0.2; $F_{1, 97} = 12.5$, $p < 0.001$). There was no effect of DISTANCE on seedling height (overall mean height: 69.9 ± 1.4 mm; $F_{1, 97} = 0.78$, $p = 0.38$). The pattern was the same in 2006, with DISTANCE affecting number of leaves per seedling (away: 9.2 ± 0.5 leaves; close: 7.5 ± 0.4 leaves; $F_{1, 78} = 9.15$, $p = 0.003$), but not seedling height (overall mean height: 97.0 ± 2.6 mm; $F_{1, 78} = 0.11$, $p = 0.74$). Neither PLATEAU nor PLATEAU × DISTANCE interactions were statistically significant for height and number of leaves in 2005 or 2006 (all p-values > 0.10).

For seedlings from gut-passed seeds in the plots, we used maternal tree level averages of all patches as control group for height, and away patches as control group for number of leaves (see paragraph above for control values). In 2005, seedlings in plots were of the same height as control seedlings (height in plots: 74.8 ± 4.6 mm, $W = 42$, $p = 0.30$; all tests: $n = 6$ plots and 20 maternal trees), and had the same number of leaves per seedling as control seedlings (number of leaves in plots: 7.8 ± 0.7 leaves, $W = 56$, $p = 0.84$). When recorded again in 2006, however, seedlings in the plots were significantly larger than control seedlings

(height in plots: 124.3 ± 13.4 mm, $W = 11$, $p = 0.002$), and still had significantly more leaves (leaves in plots: 13.4 ± 0.8 leaves, $W = 14$, $p = 0.006$).

Seedling damage

First survey

In the first survey, when we scored the damage at the leaf level for one random seedling per patch, the effect of DISTANCE was significant for overall damage level, diversity of damage, and for most of the individual damage categories. A much higher proportion of leaves was damaged close to the maternal trees, compared with seedlings further away (Fig. 5; Table 2). Apart from a marginally significant interaction with DISTANCE for the damage category scale insects, PLATEAU was not a significant main effect and did not interact with DISTANCE for any other damage category.

The occurrence of several damage categories was correlated ($n = 117$ seedlings; p-values given after sequential Bonferroni corrections). Presence of white leaf fungus was significantly correlated with presence of both leaf mines ($r = 0.27$; $p = 0.048$), curled leaf ($r = 0.28$; $p < 0.036$) and necrosis spots ($r = 0.42$; $p < 0.001$). Presence of necrosis spots was significantly correlated with presence of scale insects ($r = 0.34$; $p < 0.001$), suggesting that the former may be caused by the latter. The least well-defined damage category, discolouration, was significantly correlated with the two damage categories affecting whole leaves, white fungus ($r = 0.33$; $p < 0.001$) and curled leaf ($r = 0.29$; $p = 0.034$), and was probably the final stage in overall damage before a leaf wilted and droped off.

Compared with seedlings away from maternal trees, seedlings from gut-passed seeds had a significantly lower total proportion of damaged leaves, whereas there was no significant difference in the diversity of damage categories (Fig. 5, Table 2). While there was a trend for seedlings from gut-passed seeds in comparison with seedlings away from maternal trees to have a lower proportion of leaves damaged for almost all damage categories, the only significant difference was for necrosis spots (Fig. 5, Table 2).

Second survey

As in the first survey, we found a strong effect of DISTANCE, with seedlings in patches close ($n = 53$) to the maternal trees scoring higher overall levels of damage than seedlings in patches away ($n = 64$) from the maternal trees (means ± 1 SE; close: 2.14 ± 0.10; away: 1.62 ± 0.12; linear mixed-effects model: $F_{1,95} = 22.3$, $p < 0.001$). PLATEAU had no significant effect on

overall seedling damage level ($F_{1,18} = 1.92$, $p = 0.18$), nor was there a significant interaction between DISTANCE and PLATEAU ($F_{1,95} = 0.003$, $p = 0.95$).

There was no difference in seedling damage between the seven plots with seedlings from tortoise gut-passed seeds and the away seedling patches ($n = 64$) used as control group (gut-passed seeds: 1.57 ± 0.20, ($F_{1,25} = 0.008$, $p = 0.93$).

Seedling survival

Seedling survival from when maximum number of seedlings had germinated in a patch (ca. Nov.–Dec. 2004) to February 2006 was strongly influenced by DISTANCE and marginally by PLATEAU (Table 4). DISTANCE had a highly significant overall effect on seedling survival, with much fewer seedlings surviving close to maternal trees compared to seedlings further away. Overall, PLATEAU had a marginal effect on seedling survival, with a slightly higher seedling survival on the lower plateau. However, there was a significant interaction between PLATEAU and DISTANCE, with seedling mortality being much higher close to maternal trees on the upper plateau than on the lower plateau.

Seedlings in the seven plots had the same survival rate as seedlings in the away patches used as a control group (plots: 77.4 ± 13.9%; $F_{1,25} = 0.020$, $p = 0.89$).

Factors affecting survival

Seedling damage recorded at the patch level (second damage survey) in February 2005 was a strong predictor for subsequent mortality from February 2005 to February 2006. Seedlings in patches with low damage level survived significantly better than those in patches with medium and high damage levels (mean survival ± 1 SE; low: 90.1 ± 3.6%, $n = 40$ patches; medium: 79.2 ± 4.6%, $n = 49$ patches; high: 72.8 ± 8.9%, $n = 22$ patches; GLMM with maternal tree as random factor: $F_{1,91} = 7.72$, $p = 0.007$).

There was no significant effect of numbers of seedlings in a patch on seedling survival in that patch from maximum number of seedlings in 2004 to February 2006 (GLMM with maternal tree as random factor, and using the maximum seedling number observed per patch, $F_{1,111} = 0.36$, $p = 0.55$).

DISCUSSION

Our study investigated seed germination, seedling damage and survival, and effects of frugivore gut-passage for the critically endangered endemic Mauritian tree *Syzygium mamillatum*. We found strong negative effects of proximity to maternal trees for seedling growth and survival. This, to our knowledge, provides the first experimental evidence for a Janzen-Connell distance-dependent effect on the establishment, growth and survival of seedlings on an oceanic island. Our results clearly demonstrate the crucial importance of propagules being dispersed away from the maternal trees. The fruitless search for natural seedlings and saplings showed that there are currently no frugivorous animals acting as efficient seed dispersers of *S. mamillatum*. We demonstrate that the Aldabra giant tortoise could be used as an ecological analogue species to provide a seed dispersal service, and thus resurrect the functional component of some of the extinct endemic frugivores in Mauritius.

Seed germination, and seedling growth, damage and survival

There was no difference in germination rate or germination speed between close and away patches. However, germination rate and speed, and overall germination success were strongly affected by propagule type. For several Mauritian fleshy-fruited tree species, it has been shown that removal of the fruit pulp is important for successful seed germination; if left on ripe fruits, the pulp often gets infected by fungi that spread into the seeds and destroy them (Wyse-Jackson *et al.* 1988; Nyhagen *et al*. 2005). Seed destruction or reduced seed germination rate as a result of fungal infestations of the pulp is a common pattern found elsewhere as well (e.g. Oliveira *et al.* 1995). However, this does not seem to be the case for *S. mamillatum*. On the contrary, our results show that seeds from whole fruits germinate faster and at a higher rate than manually depulped seeds. This could be due to a high level of essential oils with anti-fungal properties found in many plants from the family of Myrtaceae (e.g. in fruits of *S. cordatum*; Pretorius *et al.* 2002). Moreover, some *Syzygium* species in Australia germinate better if fruits have been fermenting (Beardsell *et al.* 1993), and a similar effect is possible for *S. mamillatum*. Lastly, because *S. mamillatum* seeds have no hard endocarp, the pulp may protect seeds from rapid desiccation that could force them into dormancy. The latter is likely to be the main explanation in our case, as manually depulped seeds germinated more slowly and at a lower rate on the upper plateau, which is a drier and warmer habitat than the lower plateau. Seeds from whole fruits, on the other hand, germinated equally well on the upper and lower plateau.

The effects of caging on germination were more complex. Initially, the cages did protect the propagules against predation by larger animals. However, this effect was only seen for whole fruits, where initial counts of seeds (after the pulp had rotted away) were lower for non-caged than for caged patches. This is probably due to introduced ground foraging animals, such as rats or tenrecs, grabbing whole fruits in non-caged fruit patches. Caging also had a strong effect on germination speed, but only for seeds from whole fruits. This may be due to foraging animals selectively disturbing decomposing fruit (where seeds often already had started germinating, pers. obs.), and not single seeds.

Most importantly, contrary to seedling germination patterns, seedling damage levels and subsequent seedling survival were strongly affected by proximity to maternal trees. Seedlings suffered less damage and had higher survival rates when growing away from maternal trees. Furthermore, seedlings had more leaves away from maternal trees. The overall poorer growth conditions on the upper plateau, less soil of a worse quality and a drier habitat, were also reflected in seedling growth and seedling survival.

Effects of tortoise gut-passage

Despite the relatively low number of *S. mamillatum* seeds passing undamaged through the tortoises, there are at least two mitigating factors that could contribute to a high overall seedling success for gut-passed seeds in the medium to long term: Firstly, seeds are almost certainly dispersed away from areas with high seedling mortality near adult trees. Secondly, seeds are deposited in a favourable microclimate with plenty of nutrients, which leads to better growth and a lower susceptibility to natural enemies. Indeed, seedlings from gut-passed seeds did better than seedlings from both whole fruits and manually depulped seeds. They grew taller, had more leaves, and suffered less leaf damage than control seedlings in both damage surveys. The improved growth is most likely to be an effect of the extra nutrients provided by the decomposing tortoise dung. The higher nutrient status could also mean that more secondary compounds to deter natural enemies could be produced (Coley *et al.* 1985), explaining the reduction in seedling damage for *S. mamillatum* seedlings in plots.

Our estimated mean gut-passage time of two to three weeks is comparable to results from other studies of giant tortoises; Rick and Bowman (1961) reported seed gut-passage times of 10–20 days for giant Galápagos tortoises, and Hamilton and Coe (1982) found that gut-passage times for leaves and tough sedges ranged from six to 22 days. In frugivorous animals, mean gut retention time can vary depending on the amount of food consumed, and the type (e.g. wet *vs*. dry, Traveset 1998). Moreover, there could be differences between

individual tortoises (e.g. how much dry and wet food and water they have ingested, or differences in gut structure or digestion efficiency, Rodriguez-Perez *et al.* 2005).

As illustrated in Figure 4, longer gut-passage times appeared to decrease germination success. All else being equal, the seeds extracted from tortoise faeces in week five were likely to have spent longer time in tortoise guts than seeds extracted in week one. A similar trend towards lower germination success with increasing tortoise gut-passage time was noted for *Lycopersicon cheesmanii* seeds ingested by Galápagos tortoises (Rick & Bowman 1961). In contrast to large mammals and birds, large tortoises have sluggish guts with inefficient digestion (Hamilton & Coe 1982; Hailey 1997). Galápagos tortoises sometimes ingest sand, gravel or pieces of wood, and these may cause a mechanical break-up of food items that could aid digestion (Rick & Bowman 1961). Similar behaviour has been noted for two *Geochelone* species in Brazil (Moskovits & Bjorndal 1990). We did find both sand and pebbles in the faeces of the Aldabra tortoises, and it is likely that this was partly responsible for the break-up of many of the *S. mamillatum* seeds.

Compared to seeds of many other Mauritian fleshy-fruited plant species, *S. mamillatum* is probably one of the 'worst' species we could have chosen as our model organism. Its seeds have no hard endocarp to protect the cotyledons and embryo, and they therefore break apart easily. In contrast, the seeds of most other Mauritian fleshy-fruited plant species have some sort of hard seed coat. For example, on the small off-shore islet Ile aux Aigrettes, where Aldabra tortoises are used in a grazing study, they also eat the fallen fruits of the endangered *Diospyros egrettarum* (Ebenaceae). The seeds of this species have a thin but hard and smooth seed coat and pass through the tortoises unscathed, germinating very well afterwards (pers. obs.). It is therefore very likely that giant Aldabra tortoises will be able to perform well as seed dispersers of many Mauritian plant species.

Many experimental seed dispersal studies fail to test germination of gut-passed seeds *in situ*; that is, embedded in the faeces. These studies extract seeds from the faeces and germinate them in another environment than the one they would have been exposed to in a natural situation. Obviously, the influence of faecal matter is likely to differ greatly between different frugivore species and seeds from different plant species. For example, the relatively fluid composition of most bird droppings is unlikely to create or sustain a particular microclimate around excreted seeds for longer periods of time. In contrast, a tortoise turd is much more substantial, maintaining structural integrity and creating a specific microclimate for a longer period. The responses of different seeds to different types of scat are likely to

depend on many factors and be idiosyncratic with respect to both plant species and frugivore species.

In any study that aims to investigate seed germination and seedling establishment and the influence of gut-passage on endangered species in conservation areas, it is important to do so in the field, rather than in nurseries or greenhouses, where conditions can be very different from those in the field. Rodriguez-Perez *et al.* (2005) found that germination rates of a species after gut-passage through birds and lizards could vary greatly between field- and garden sites, sometimes with completely opposite patterns. Furthermore, it is important to include all possible control groups to seeds from gut-passage experiments; that is, not only manually depulped seeds but also whole fruits or infructescences, a setup that is regrettably still not the norm in most experimental seed dispersal studies (Samuels & Levey 2005). Failure to use a proper protocol may lead to wrong recommendations for future conservation management strategies.

Janzen-Connell patterns on Mauritius and other oceanic islands

Our results clearly demonstrate that the predictions of the Janzen-Connell model apply to seedling survival of *S. mamillatum* in Mauritius. However, more studies on other plant species in Mauritius, and above all, more studies on other oceanic islands are needed before any generalisations can be made. With our study, we were able to identify some of the potential drivers of Janzen-Connell patterns in *S. mamillatum* seedling damage and subsequent mortality. Parts of the damage were clearly related to activity by insects (mines, scale insects and probably most of the small necrosis spots) and fungi (white fungus and maybe curled leaves). Interdependence of damage categories is very likely, and we found significant correlations between occurrences of several seedling damage categories (Table 3). For example, the presence of leaf fungus was significantly correlated with presence of two of the mechanical damage categories, leaf mines and necrosis spots. This is in line with another study, which showed that fungal pathogens in a tropical rainforest required insect damage to infect plants (García-Guzman & Dirzo 2001).

Of course, we cannot be sure that seedling damage and mortality is primarily related to natural enemies, rather than, for example, seedling competition. However, the patterns of increased damage were evident even in the patches with one solitary seedling or few seedlings that did not grow in a tight clump. Here, seedling densities are likely to be below levels that could lead to seedling competition (Clark & Clark 1984). In fact, it has been suggested that competition for resources between seedlings is unlikely to be a major contributor to seedling

mortality in tropical forests, at least for young seedlings (Wright 2002, Bell *et al.* 2006). Therefore, it is most likely that the differences in *S. mamillatum* seedling damage and mortality in relation to distance from maternal trees are a result of corresponding differences in levels of natural enemies near to and away from maternal trees.

Specialist or generalist natural enemies as drivers of Janzen-Connell patterns in Mauritius and other oceanic islands?

We were not able to identify the natural enemies that caused the seedling damage. This is an obvious limitation of our study, and more investigations on identity and specificity of natural enemies of plants on islands are much needed (Ribeiro *et al*. 2005). Therefore, we cannot speculate on the overall relative importance of generalists and specialists in our study system. However, if host-specificity of natural enemies in Mauritius is apparent at the family or genus level, which is often the case for insect herbivores in tropical forests (Novotny & Basset 2005), then *S. mamillatum* and other endangered Myrtaceae species in Mauritius may be especially vulnerable. Two of the main invasive plant species in Mauritius are from the same genus and family as *S. mamillatum*, respectively (*S. jambos* and *Psidium cattleianum*). These abundant invasives could act as reservoirs of natural enemies in the invaded parts of the forest, which could lead to a high migration rate of natural enemies into the CMAs.

In general, islands are often said to harbour simple ecosystems, in which case we could expect more generalist than specialist natural enemies. However, even generalist natural enemies can also be density- or even distance-responsive (Janzen 1970, Clark & Clark 1984). Moreover, with increasing age, islands harbour more species-rich and complex plant communities. In turn, this creates more niches for specialised herbivores. The incidence of specialist herbivores on an oceanic island is therefore likely to depend on the age of the island (e.g. Borges & Brown 1999, Gillespie & Roderick 2002). As a result, we may expect to find specialist-driven Janzen-Connell patterns more often on old than on young oceanic islands. More studies on the prevalence of generalist and specialist natural enemies on oceanic islands, and how they affect regeneration of plant species, are clearly needed.

The use of ecological analogue species to resurrect lost seed dispersal interactions on oceanic islands

In our study, we assessed the use of Aldadra tortoises by using captive animals for feeding experiments, and subsequently deposited seeds and faeces in the CMA. This is a good approach for initial assessments of the suitability and functioning of ecological analogue seed

dispersers. However, it contributes only little to restoring natural dynamics in the forest. Ultimately, we need to release candidate ecological analogue species into the habitat in which we want to resurrect the lost interactions. Translocated Aldabra tortoises on Curieuse Island readily ate fruits of plants they had not encountered before (Hambler 1994). However, they dispersed seeds of invasive species, too, but this would not pose a problem within the weeded CMAs in Mauritius. One major advantage of using giant tortoises as ecological analogues is that it is relatively easy to monitor them, and if necessary to add or remove tortoises, thus adjusting their impact on the habitat (Jones 2002).

When selecting candidate species for release as ecological analogues within conservation management areas on oceanic islands, there are several important points to consider. Firstly, although it may be tempting to look for the closest living relative of the extinct species, an evolutionarily close extant species is not necessarily a good ecological analogue (Jones 2002). That is, close taxonomical affinity does not automatically translate into ecological similarity. This is in particular the case on oceanic islands, which are famous for the large number of adaptive radiations. Secondly, it would not make sense to release ecological analogue species without having addressed the factors that resulted in the extinction of the original species (Fischer & Lindenmayer 2000). The latter point is already the main focus of many CMAs on oceanic islands; introduced predators and competitors have been eradicated or are being controlled or excluded, especially on smaller offshore islets and fenced habitats on main islands (e.g. Towns *et al.* 1990, Jones & Hartley 1995, Nogales *et al.* 2004).

It is ironic that one of the first and best known but poorly executed studies of a plant and its extinct seed disperser – and the use of an ecological analogue species to replace it – is from Mauritius. The famous Dodo and Tambalacoque story (Temple 1977) has been cited frequently in the ecological literature as an example of a disrupted mutualism, but suffers from serious flaws (Witmer & Cheke 1991, Cheke & Hume in press), and fails by a large margin to demonstrate anything like the ‘obligatory mutualism’ it suggests. There is more than one candidate ‘ghost’ in the Mauritian frugivore fauna that could have dispersed the Tambalacoque seeds; giant tortoises or giant skinks, for example (Iverson 1987, Witmer & Cheke 1991). There are even extant fruitbats that are capable of dispersing the large fruits (V. Florens, pers. comm.). This story does serve to prove a very important point, though: Most seed dispersal mutualisms are not specialised. Only rarely does one plant species depend on one animal species for dispersal, and only rarely does one frugivore depend on one plant species for food (Howe & Smallwood 1982). Hence, one ecological analogue species is likely

to benefit more than one plant species. By using ecological analogue species, practical conservation management and ecological and evolutionary studies on the nature of seed dispersal interactions may complement each other.

Conclusions

Many studies have pointed out the important roles of either disrupted seed dispersal mutualisms (e.g. Bond 1994, Traveset & Riera 2005) or natural enemies (Gilbert & Hubbell 1996, Bevill *et al.* 1999) in the conservation of rare plants. With our study we highlight the combined potentially greater importance of both for endangered plants on oceanic islands compared to mainland habitats. Conservation management of endangered plants on oceanic islands should take the potential importance of both missing seed dispersers and resulting Janzen-Connell patterns in seedling growth and mortality into account. We suggest that one way of mitigating a lack of dispersal and improving seedling performance is to use ecological analogue frugivorous species *in situ*. Furthermore, it is important for future studies to expand on the importance of Janzen-Connell patterns in conservation management areas in Mauritius and other oceanic islands to include other, more numerous species, to be able to investigate density- as well as distance-dependent effects (Wills *et al.* 1997).

Lastly, our suggestions for using ecological analogue species in the conservation management of endangered oceanic island species may be expanded to mainland habitat fragments, which often suffer from locally extinct seed dispersal interactions (e.g. Cordeiro & Howe 2001, Galetti *et al.* 2006).

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TABLES

Table 1 Summary of the GLMM used to analyse *Syzygium mamillatum* seed germination patterns over time (see also Fig. 3). Statistically significant *p* values (<0.05) are indicated in bold. *df* = numerator degrees of freedom, denominator degrees of freedom.

	df	*F*	*p*
PLATEAU	1, 18	0.55	0.47
DISTANCE	1, 130	0.27	0.61
PROPAGULE	1, 130	11.5	**0.0009**
CAGE	1, 130	1.92	0.17
TIME	1, 772	482	< **0.0001**
PLATEAU × DISTANCE	1, 130	0.04	0.84
PLATEAU × PROPAGULE	1, 130	6.19	**0.014**
DISTANCE × PROPAGULE	1, 130	0.03	0.86
DISTANCE × CAGE	1, 130	0.04	0.83
PLATEAU × CAGE	1, 130	1.68	0.20
PROPAGULE × CAGE	1, 130	5.11	**0.025**
PLATEAU × TIME	1, 772	0.03	0.86
DISTANCE × TIME	1, 772	0.40	0.53
PROPAGULE × TIME	1, 772	9.75	**0.002**
CAGE × TIME	1, 772	5.34	**0.021**
PROPAGULE × CAGE × TIME	1, 772	5.15	**0.024**

Table 2 First seedling damage survey. The three first lines summarise the nine GLMMs used to analyse the first survey of damage for propagule seedlings, while the lowest line summarises the nine GLMMs used to compare damage levels of seedlings from gut-passed seeds in plots to seedlings in away patches. Statistically significant *p* values (<0.05) are indicated in bold. *df* = numerator degrees of freedom, denominator degrees of freedom.

		Total		Diversity		Leaf mine		Fungus		Curled leaf		Bite damage		Necrosis spot		Scale insect		Discolouration	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
PLATEAU	1, 18	0.46	0.51	0.01	0.94	0.20	0.66	0.11	0.74	0.03	0.88	1.04	0.32	0.08	0.78	0.55	0.47	0.24	0.63
DISTANCE	1, 93	11.3	**0.001**	3.72	*0.057*	0.44	0.51	10.9	**0.001**	9.70	**0.002**	7.36	**0.008**	6.01	**0.016**	2.85	*0.094*	5.73	**0.019**
PLATEAU × DISTANCE	1, 93	0.79	0.38	0.67	0.42	1.60	0.21	1.62	0.21	0.12	0.73	2.57	0.11	0.88	0.35	2.96	*0.089*	0.14	0.71
Gut-passed vs. away	1, 25	7.36	**0.012**	0.96	0.337	2.76	0.109	0.70	0.410	0.11	0.749	0.20	0.659	9.01	**0.006**	0.01	0.944	1.26	0.272

Table 3 Seedling survival from when maximum number of seedlings had germinated in a patch in November–December 2004 to February 2006, with corresponding test statistics from the GLMM analysis. Percentage survival is expressed as means ± 1 SE at level of the 20 maternal trees, with 15 trees on the lower and 5 trees on the upper plateau. Statistically significant *p* values (<0.05) are indicated in bold. *df* = numerator degrees of freedom, denominator degrees of freedom.

Effects	Levels	Survival (%)	*df*	*F*	*p*
PLATEAU	upper	54.9 ± 7.1	1, 18	3.54	0.076
	lower	66.8 ± 4.0			
DISTANCE	away	78.1 ± 3.8	1, 110	29.5	< **0.001**
	close	48.0 ± 6.6			
PLATEAU × DISTANCE	upper, close	24.5 ± 11.9	1, 110	10.4	**0.002**
	lower, close	55.7 ± 6.2			
	upper, away	88.0 ± 3.7			
	lower, away	75.2 ± 4.6			

FIGURES

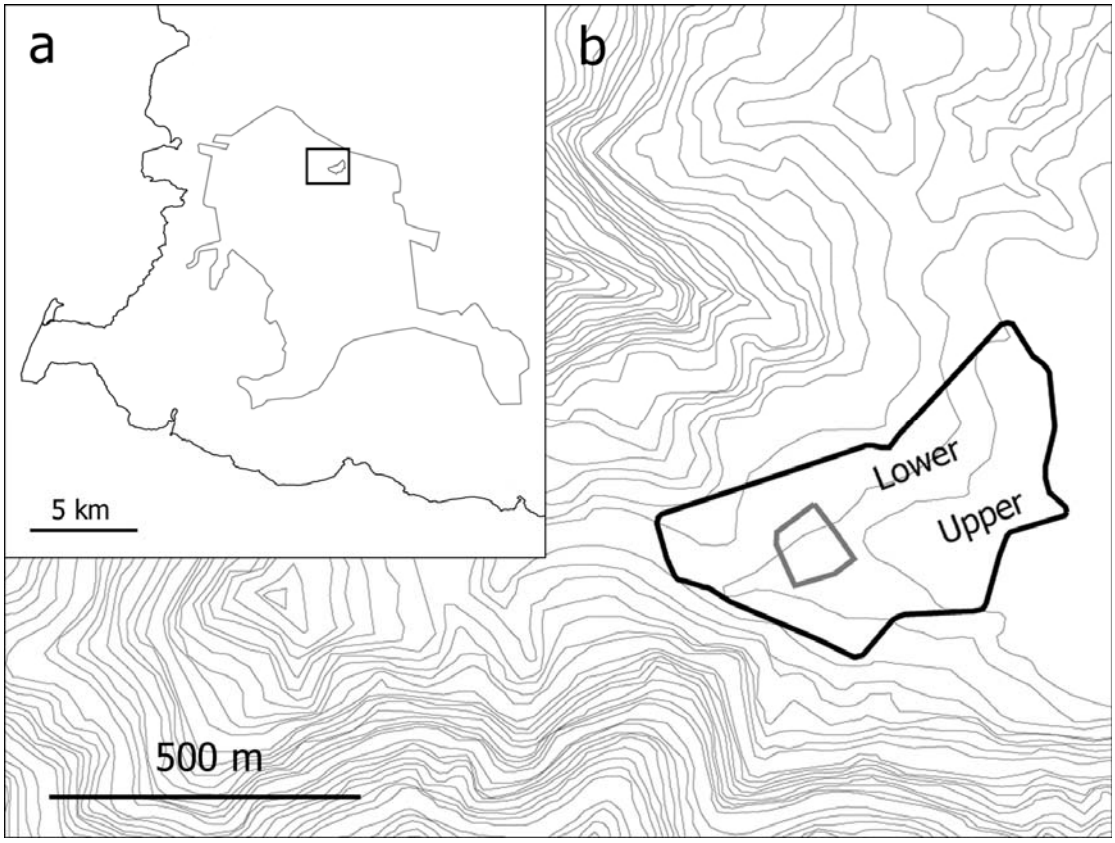

Figure 1 (a) Map of the south-western corner of Mauritius, with the borders of the Black River Gorges National Park outlined in grey, and the enlarged part in (b) indicated with a small rectangle. (b) Brise Fér plateau with topographical curves. Each curve represents a change in altitude of 10 m. The fenced CMA is outlined in black, with the oldest weeded part ('Old Plot') outlined in grey. The upper and lower plateaus of the eastern part of the CMA, where most of the *Syzygium mamillatum* trees are found, are labelled as 'Upper' and 'Lower', respectively.

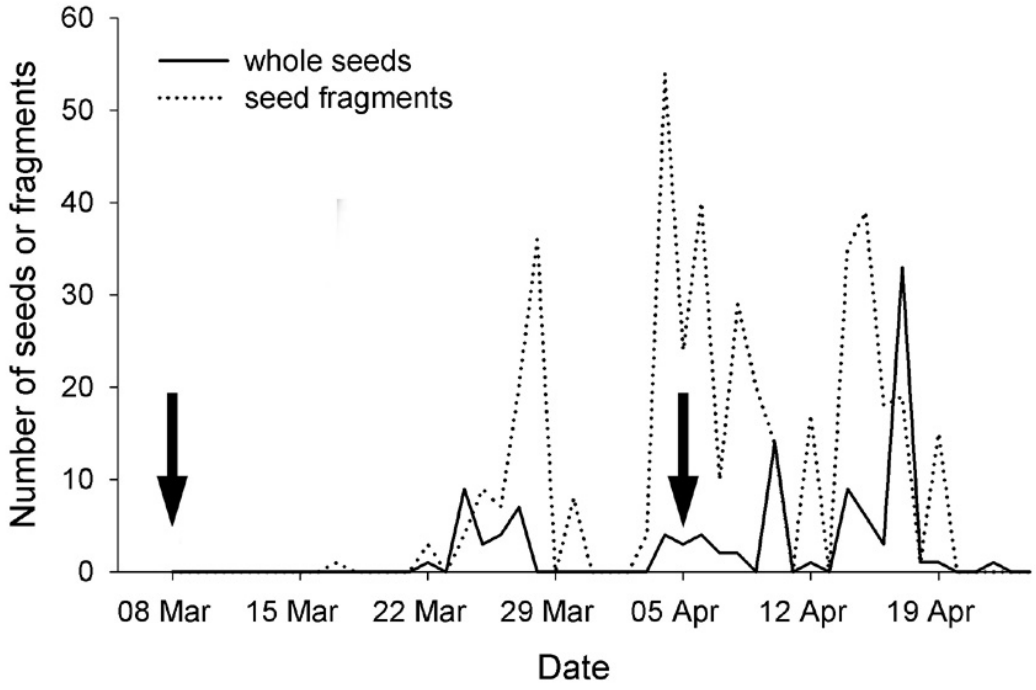

Figure 2 Gut-passage and excretion patterns of seeds and seed fragments from *Syzygium mamillatum* fruits fed to giant Aldabra tortoises. The two arrows indicate the beginning and the end of the feeding period, respectively.

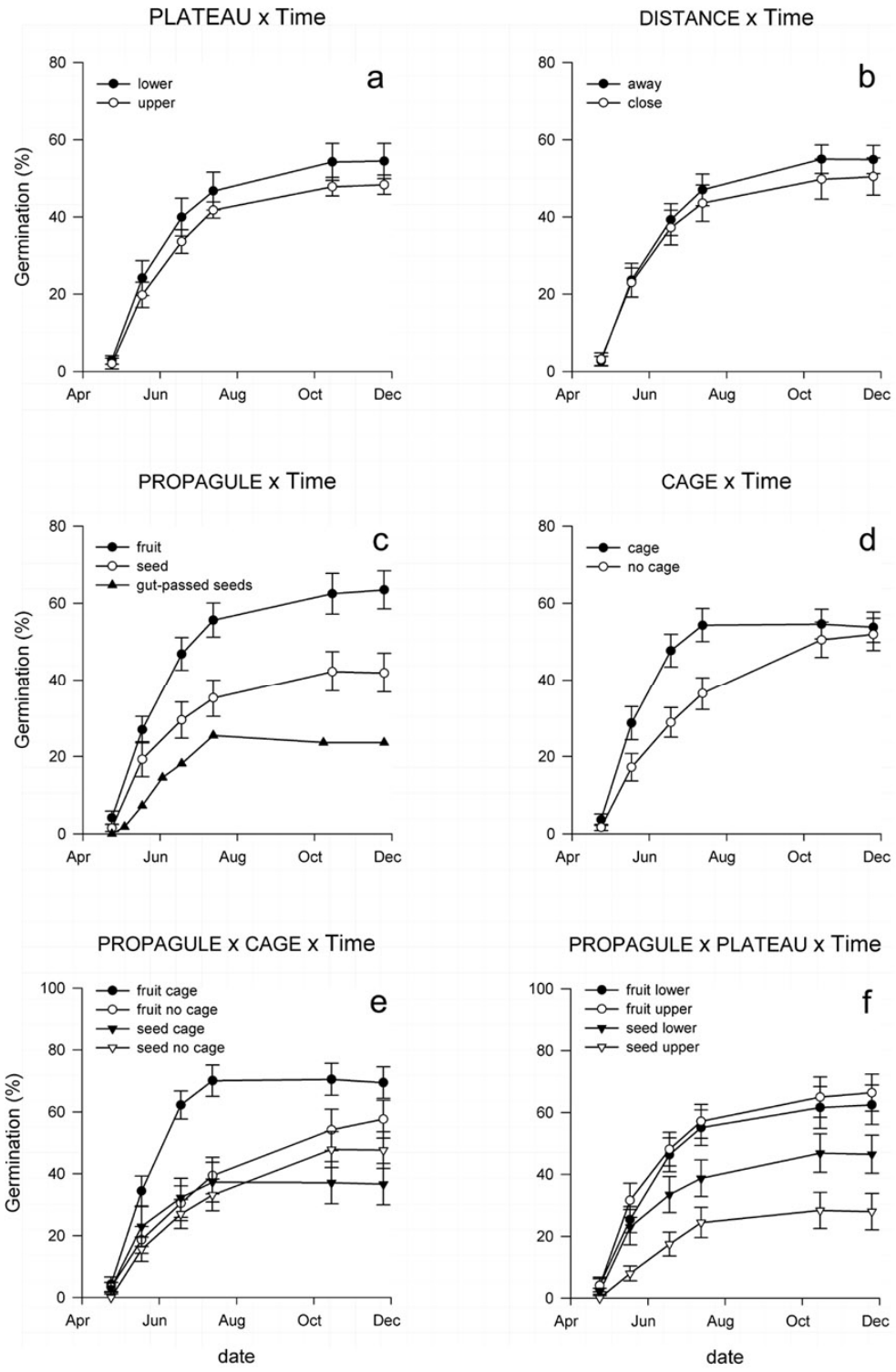

Figure 3 Seed germination patterns of *Syzygium mamillatum*. (a)–(d) illustrates the interactions with Time for each of the main effects (see Table 1). Values plotted are means ± 1 SE at the maternal tree level (n = 20 trees, except for PLATEAU which a sample size of 15 maternal trees on the lower plateau, and five maternal trees on the upper plateau). In (c), we have added the germination pattern of tortoise gut-passed seeds (overall proportion, seeds and seedlings pooled from all 12 gut-passed seed plots). (e) and (f) illustrate the significant higher-order interactions from Table 1.

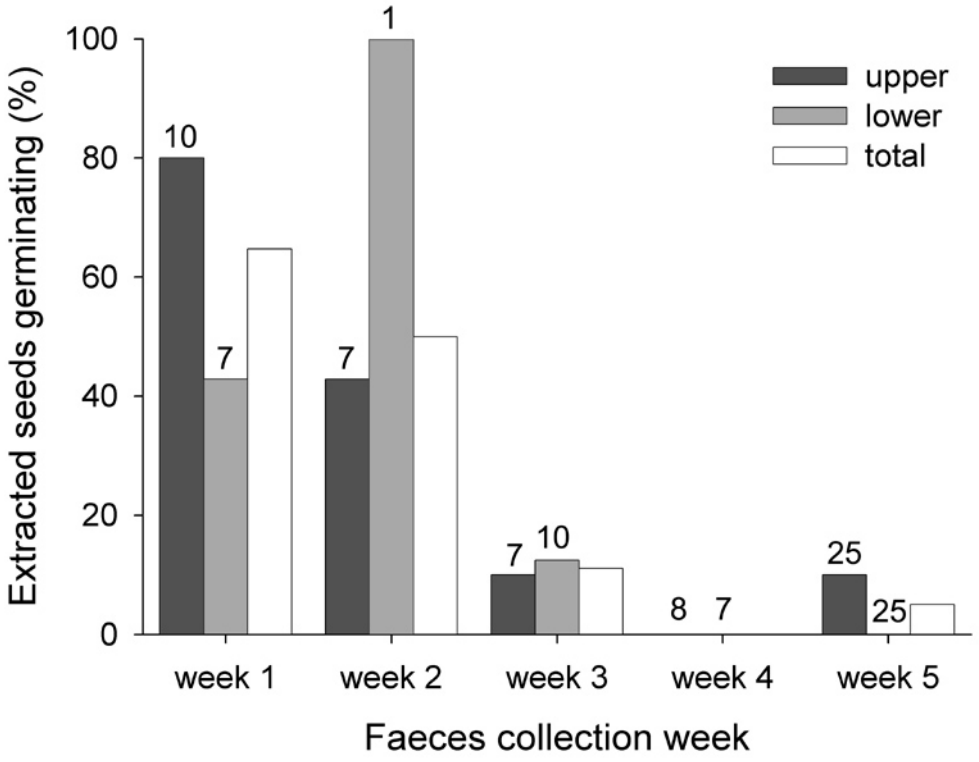

Figure 4 Percentage of tortoise gut-passed seeds germinating in relation to collection week. Numbers above the bars are the number of seeds sown in the forest on the upper and lower plateau, respectively.

CHAPTER 4

Are there negative indirect effects between endemic and invasive flowering plant species via shared pollinators?

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(submitted to *Biological Invasions*)

ABSTRACT

In generalised plant–pollinator systems, the addition of invasive, exotic plant species may disrupt native, co-evolved plant–animal interactions, resulting in reduced reproductive success of native plant species. We tested this concept in a field study in Mauritius, where the invasive strawberry guava *Psidium cattleianum* provides additional floral resources for pollinators in the form of large amounts of pollen. We predicted that the presence of flowering guava plants would indirectly and negatively affect the reproductive success of the endemic plant *Bertiera zaluzania* by appropriating shared pollinators. We removed *P. cattleianum* flowers from around half the *B. zaluzania* target plants (treatment), and left *P. cattleianum* flowers intact around the other half (control). By far the most abundant and shared pollinator was the introduced honey bee, *Apis mellifera*, but its visitation rates to treatment and control plants were similar. Likewise, fruit and seed set, and fruit size and weight of *B. zaluzania* were not influenced by the presence of *P. cattleianum* flowers. Despite the lack of evidence for negative indirect interactions in our system, the dominance of introduced *A. mellifera* and the lack of native pollinators of *B. zaluzania* suggest a disruption of native plant–pollinator interactions.

INTRODUCTION

Introduced species may utilise biotic interactions to successfully invade a natural community (Orians 1986, Mack *et al.* 2000), and a general knowledge of such new associations among species is fundamental to understanding invasion processes (Parker *et al.* 1999). Biotic interactions are indirect when the impact of one species on another is mediated by the presence of a third species of a different trophic rank (Holt 1977). Indirect interactions between flowering plants occur when two plant species compete for a common pollinator, with negative consequences for the reproductive success of one or both species (Waser 1983, Campbell & Motten 1985). For example, pollinators may neglect certain flowering species because neighbouring plants offer larger amounts of nectar (Chittka & Schürkens 2001), or pollinators may transfer large quantities of heterospecific pollen that interfere with fertilisation by conspecific pollen (Waser 1978, Campbell & Motten 1985, Feinsinger 1987). Such situations are possible when exotic flowering plant species invade new plant communities and start interacting indirectly with neighbouring, resident species (Thomson 1982, Richardson *et al.* 2000, Ghazoul 2004). Indirect interactions can also be positive and lead to an increase in reproductive success of one flowering plant species in the presence of a second, which offers rewards to shared pollinators (Thomson 1982, Rathcke 1983, Feldman *et al.* 2004, Ghazoul 2006). For example, Johnson *et al.* (2003) showed that plant species providing large quantities of nectar increased the local abundance of pollinators and, as a consequence, the co-occurring, non-rewarding orchid *Anacamptis morio* experienced higher pollination success.

Ecological studies on entire pollinator assemblages suggest that symmetric specialisation (i.e. specialist pollinators interacting with a specialist plants) may be the exception rather than the rule (e.g. Waser *et al.* 1996, but see Johnson & Steiner 2000), and asymmetric specialisation (i.e. specialists interacting with generalists) is a common feature of most plant–pollinator systems (Vázquez & Aizen 2004, Bascompte *et al.* 2006). This generalisation in pollination systems results in pollinators sharing floral resources, which is essential for indirect interactions to occur among flowering plants. Little is known about the role of indirect interactions among flowering plants mediated by pollinators in determining community composition of flowering plants (e.g. Levin & Anderson 1970), and evidence from experimental studies is rare (but see Waser 1978, Chittka & Schürkens 2001, Moeller 2004). Indirect interactions may become particularly important when exotic plant species invade native habitats and cause disruptions or shifts in native co-evolved pollination systems.

Exotic plants which colonise new habitats beyond the range of their original pollinators may only succeed by interacting with new, resident generalist pollinators.

Negative effects, such as displacement of native plant species by invasive plants, are well-documented for island ecosystems (Smith 1985, Simberloff 1995, Daehler 2003). In addition, island pollination systems are usually generalised (Olesen *et al.* 2002, Dupont *et al.* 2003), because only a subset of mainland pollinators has colonised island habitats. This selective colonisation results in relatively depauperate faunas compared to mainland pollinator communities (MacArthur & Wilson 1967, Feinsinger 1987). Therefore, introduced generalist pollinators and plants which attract a wide range of pollinators have a higher chance of success of invading island pollination systems (Simberloff & von Holle 1999, Richardson *et al.* 2000). The role of indirect interactions between invasive and native plant species in generalised systems, however, has not been studied intensively, and results are conflicting (e.g. Aigner 2004, Moragues & Traveset 2005).

We studied indirect interactions between an invasive and an endemic flowering plant species on the oceanic island of Mauritius. Mauritius has experienced multiple plant and animal invasions (Mauremootoo *et al.* in press), which have contributed to the degradation of native forests and reduced the population sizes of many native plant species (Page & d'Argent 1997). As on many other islands, Mauritius has generalised pollination systems (predominantly flies, CN Kaiser unpublished data) and there is a paucity of pollinator species (Hansen *et al.* 2002). We experimentally studied the impact of the abundant flowers of invasive strawberry guava *Psidium cattleianum* Sabine (Myrtaceae) on the reproductive success of the endemic plant, *Bertiera zaluzania* Gaertner f. (Rubiaceae) on a local scale. *Bertiera zaluzania* was selected as the target species for several reasons. Firstly, it is a typical representative of the Rubiaceae family, which contains 59 native species in Mauritius, 29 of which are listed as endangered or critically endangered according to IUCN criteria (Baillie et al. 2004); secondly, *B. zaluzania* has similar floral and phenological characteristics to *P. cattleianum*; and thirdly, both plant species have white, easily accessible flowers and were assumed to share generalist pollinators. We hypothesised that (*1*) the removal of *P. cattleianum* flowers changes the visitation rate of pollinators to *B. zaluzania*, (*2*) pollinators visiting *B. zaluzania* without surrounding *P. cattleianum* flowers carry less heterospecific pollen than those visiting *B. zaluzania* surrounded by *P. cattleianum* flowers, and (*3*) the change in visitation rate to *B. zaluzania* results in altered reproductive success of *B. zaluzania*.

MATERIALS AND METHODS

Study sites

Our study was conducted at Plaine Champagne, a part of the central upland plateau of the 6754 ha Black River Gorges National Park in Mauritius (20°42' S, 57°44' E). The study site is a remnant area of approximately 9 ha of diverse heathland community that was formerly widespread throughout the upland plateau. During the last century, the area has been heavily invaded by exotic plant species, such as *Psidium cattleianum,* privet *Ligustrum robustum* Blume (Oleaceae), and *Wikstroemia indica* Mey (Thymelaeaceae), which now dominate the habitat. The field work was carried out between November 2003 and May 2004, which covered the second half of the main flowering season with approximately 75% of native and 90% of introduced plant species flowering and fruiting during this period.

Study organism and floral traits

The introduced strawberry guava *P. cattleianum* is one of the most invasive weeds in the upland forests of Mauritius, and its peak flowering season in the upland region lasts from November to December. *Psidium cattleianum* is hermaphroditic and displays open white flowers with a diameter of *ca*. 3.5 cm and several hundred anthers. Flowers of *P. cattleianum* produce no nectar, as inferred by sampling total nectar crop with 5 µl glass microcapillaries from a total of 35 flowers on 11 plants on several days.

The endemic plant species *Bertiera zaluzania* is a functionally dioecious, perennial shrub of *ca*. 2 m height, which protrudes above the lower thicket of *P. cattleianum*. Heterostylous male and female flowers are morphologically different. Female flowers of *B. zaluzania* stay viable for a maximum of one day, often with the stigma being observed to wilt at around noon. Flowers of *B. zaluzania* are displayed in inflorescences of up to 150 flowers, each flower *ca*. 1.5 cm in diameter. Flowering of *B. zaluzania* occurs from November to January and fruiting from March to April. Fruits contain up to 300 seeds each. Flowers produced, on average, 2.8 ± 0.4 SE µl nectar with a sugar concentration of 16.3 ± 0.4 % (n = 45), as determined from 105 newly opened flowers (20 female and 25 male) between 7.00 am and 9.00 am with a hand-held refractometer (Eclipse 45-81, Bellingham & Stanley). Functional male and female flowers produced nectar of similar quantity ($F_{1,43} = 3.08$, $p = 0.086$) and sugar concentration ($F_{1,43} = 1.33$, $p = 0.225$). We found no pollen grains on the anthers of seven functionally female plants, while those of seven male plants contained 16315 ± 6455 pollen grains. The number of pollen grains was determined by light microscopy using a counting chamber.

Indirect effects between plant species: experimental design

We selected 20 single-standing, female *B. zaluzania* target plants surrounded by dense stands of *P. cattleianum*. The target plants were assigned randomly to two experimental groups of 10 plants each. In one group (treatment), all *P. cattleianum* flowers and buds within a circle of 5 m radius (or an area of 78.5 m^2) were removed before flower initiation of *B. zaluzania*. In the other group (control), *P. cattleianum* flowers and buds around *B. zaluzania* were not removed. No other plant species were flowering within this 5 m radius. The removal of *P. cattleianum* flowers in an area of 78.5 m^2 around the target plant was considered to be sufficient to show indirect effects on a small scale.

To determine the reproductive success of *B. zaluzania*, we counted buds and inflorescences of target plants at the beginning of the experiment and then counted the developing fruits two weeks after wilting of the last flower in January 2004. Eight weeks later, in March 2004, we collected a total of 705 ripe fruits from all target plants, measured their weight and size, and recorded the number of seeds in a sub-sample of the collected fruits (n = 532). We defined fruit set as the proportion of buds developing into fruits and seed set as the mean number of seeds per fruit. Seed set may partly be an indicator of pollination efficiency, as the number of pollen grains deposited on the stigma is usually related to the number of seeds produced by the fruit (Silander & Primack 1978, Campbell 1986), for example Kohn and Waser (1985) described a non-linear, asymptotic relationship between seed set and the number of pollen deposited on the stigma.

Pollinator activity

Pollinator observations on *B. zaluzania* were conducted on nine sunny days between 28th November and 22nd December 2003. Flower visitors to five *B. zaluzania* plants of the treatment group and to six plants of the control group were recorded. Total observation time was 32 half-hour 'observation units'. All observations were carried out between 7.00 am, when the first flowers opened, and dusk at 6.00 pm. When accurate visitor identification was impossible by sight alone, insects were caught for later identification. For each observation unit, we counted the number of flowers observed in order to calculate visitation rate, which was defined as the number of visits flower^{-1} hour^{-1}. Flower visitors were only recorded when they touched the receptive parts of the flower. *Psidium cattleianum* flowers and buds were counted in 10 random quadrats (0.25 m^2) within each circle around *B. zaluzania* control plants to estimate the number of guava flowers and buds within the experimental patch of *ca*. 78.5 m^2 (5 m radius).

Pollen load on insects

To estimate the level of heterospecific pollen transfer, we collected 35 flower visitors before they entered flowers of *B. zaluzania.* The insects were collected from the target plants but not during pollinator observations. Each insect was wiped with a 0.25 cm^2 piece of fuschin gel (Kearns & Inouye 1993) to collect pollen from the head, the ventral and dorsal sides of the thorax, and the abdomen. The gel was melted onto a microscope slide and covered with a glass cover slip. Pollen grains were identified and counted using light microscopy (see also Appendix CD).

Data analysis

We analysed differences among treatments using ANOVAs (statistical package R 2.1.1, R Development Core Team 2005). To fulfil the assumptions of normality and homoscedasticity of residuals, we transformed the response variables 'visitation rate' reciprocal, 'fruit set' arcsine-square-root, 'seed set' $\log_{10}$, and both pollen loads and 'number of pollen grains' from *B. zaluzania* and *P. cattleianum* $\log_{10}$, following the suggestions of Box-Cox transformation tests (Quinn & Keough 2002). To test for differences between numbers of pollen grains from different plant species carried by flower visitors, we ran a two-way ANOVA with individuals and treatment as factors. Non-parametric tests were used if assumptions of normality and homoscedasticity of residuals could not be met by data transformation. The relationship between fruit and seed set and the effect of treatment on this relationship were analysed by ANCOVAs. All means ± standard errors displayed in the figures were calculated from untransformed data.

RESULTS

Pollinator activity

A total of seven visitor species were recorded on flowers of *B. zaluzania* (Table 1). The honey bee *Apis mellifera* was by far the most common, with 95% of all visitations to *B. zaluzania*, and visited flowers of both treatment and control plants. Other species were observed visiting flowers only nine times, and none of the observed visitors occurred at both treatment and control plants (Table 2). Visitation rates to control (1.01 ± 0.48 visits $flower^{-1}$ $hour^{-1}$) and treatment (0.65 ± 0.30) plants were not significantly different ($F_{1,9} = 0.09$, $p = 0.76$). Visitation rates in the morning and the afternoon were also similar ($U = 35.0$, $n = 16$, $p = 0.923$). On *P. cattleianum* flowers we observed mainly honey bees and single individuals of

other insect species foraging for pollen (Bombyliidae flies *Villa unifasciata* and pollen feeding beetles *Chaetocnema* sp.).

Pollen loads on insects

Overall, flower visitors to *B. zaluzania* (20 *Apis mellifera* (Apidae), 6 *Villa unifasciata* (Bombyliidae), 3 *Allograpta nasuta* (Syrphidae), 3 *Chaetocnema* sp. (Chrysomelidae), 2 Curculionidae, and 1 *Pristomerus* sp.(Hymenoptera)) carried significantly fewer conspecific pollen grains than pollen of *P. cattleianum* and unidentified plant species (*Bertiera*: 2.17 ± 0.47, *Psidium*: 65.7 ± 40.3, Other: 17.2 ± 6.72; $F_{\text{individuals } 2,68} = 2.21$, $p = 0.003$, $F_{\text{treatment } 2,\ 68} = 14.42$, $p < 0.001$). The total number of pollen grains carried by flower visitors to treatment and control groups was only marginally different ($F_{1,33} = 3.12$, $p = 0.086$), with slightly more pollen grains found on insects visiting control plants. Flower visitors to treatment plants carried significantly fewer conspecific pollen grains than visitors to control plants (1.20 ± 0.47 *vs*. 3.46 ± 0.8; $F_{2,\ 68} = 8.28$, $p = 0.007$). The pollen loads from other plant species were similar between groups, although there was a trend towards more *P. cattleianum* pollen on insects visiting control plants ($F_{1,33} = 3.66$, $p = 0.065$; Fig. 1). As *A. mellifera* was the most common flower visitor in our study, we compared pollen loads of honey bees visiting the two treatments. Honey bees visiting flowers on treatment plants carried significantly fewer pollen grains of *B. zaluzania* than those on the control plants ($F_{1,18} = 5.12$, $p = 0.036$).

Reproductive success

Psidium cattleianum plants produced, on average, 10,383 (± 790) flowers and buds within the 5 m experimental radius around *B. zaluzania* control plants. Due to a fungal infestation, one plant of the control group lost all its buds and flowers and was therefore excluded from further analyses. Reproductive success of *B. zaluzania* did not differ between treatment and control plants. Neither fruit set nor seed set were significantly different between treatment and control plants. *Bertiera zaluzania* produced a mean fruit set of 53.0 (± 5.9) percent (range: 10–81%) in treatment and a mean fruit set of 51.3 (± 2.4) percent (range: 39–63%) in control plants, which was not significantly different between treatment and control plants ($F_{1,17} = 0.52$, $p = 0.48$). Similarly, mean seed set of 84.0 (± 12.0) of treatment plants did not differ from the mean seed set of 82.5 (± 7.76) of the control plants ($F_{1,17} = 0.028$, $p = 0.87$). Overall, fruit and seed set were positively related ($F_{1,16} = 6.47$, $p = 0.02$, $R^2 = 0.29$), but there was no effect of treatment ($F_{1,16} = 0.09$, $p = 0.77$). There was no relationship between fruit set and the number of *P. cattleianum* flowers in the control group ($R^2 = 0.01$, $n = 9$, $p = 0.79$). No

significant differences between treatment and control plants were observed for other reproductive traits, such as fruit size, number of inflorescences per plant or number of buds per inflorescence (Table 2). However, fruits of control plants were marginally heavier (p = 0.06) compared to treatment plants.

DISCUSSION

We found the removal of *P. cattleianum* flowers to have no detectable effect on the number of visitors to *B. zaluzania*, or on the overall amount and composition of pollen carried by the visitor, although there was more conspecific pollen on visitors to control plants. Most importantly, we detected no difference in fruit and seed set between treatment and control plants. Nevertheless, the relationship between fruit and seed set varied more in the absence of *P. cattleianum* flowers. We conclude that the reproductive success of *B. zaluzania* was not affected by small-scale indirect interactions between co-occurring *B. zaluzania* and *P. cattleianum*. Previous studies have shown similar neutral effects (e.g. Aigner 2004), but findings of positive (Moeller 2004, Ghazoul 2006) and negative effects (e.g. Brown & Mitchell 2001) have also been described.

The absence of indirect interactions between the invasive *P. cattleianum* and the rare, declining *B. zaluzania* is encouraging, as this suggests that *P. cattleianum* does not constitute an additional threat to *B. zaluzania* and potentially other native plant species by amplifying indirect competitive effects via mutualists. The primary impact of *P. cattleianum* on native plant species may be direct competition for nutrients, space, and light (Huenneke & Vitousek 1990). This competition is likely to have contributed to a decline in population size and relative abundance of *B. zaluzania* throughout the upland of Mauritius (Page & d'Argent 1997). The removal of *P. cattleianum* flowers and buds around *B. zaluzania* treatment plants may have caused a vegetative compensatory growth of *P. cattleianum* (e.g. Järemo *et al*. 1996). This could lead to increased competition for soil nutrients and water, and may explain the trend towards production of lighter fruits by treatment plants compared to control plants. However, detailed soil nutrient analyses would be necessary to support this hypothesis.

Surprisingly little is known about the reproductive biology of *P. cattleianum*, but the congeneric *P. firmum* of Brazil is self-compatible and visited by a variety of bee species (Proença & Gibbs 1994). During the initial invasion process of *P. cattleianum* in Mauritius, honey bees may well have played a crucial role in its success. There is evidence that mutualists can enhance the competitive abilities of invaders (Simberloff & von Holle 1999, Richardson *et al.* 2000, Morales & Aizen 2002). A study in California and on Santa Cruz

Island showed that the invasion of yellow star-thistle *Centaurea solstitialis* is facilitated by interactions with the non-native *A. mellifera* (Barthell *et al.* 2001). The combined invasion of plants and mutualistic partners will ultimately also benefit the animal mutualists. Honey bees were introduced to Mauritius approximately 300 years ago (Staub 1993). The presence of the invasive *P. cattleianum* could have facilitated the establishment of feral honey bees in natural sites. Consequently, the original pollinator community may have undergone displacement and extinction through competition with the highly abundant honey bees for floral resources (e.g. Paton 1993, Butz Huryn 1997, Paini 2004). Indeed, displacement of native pollinators by honey bees is common in many degraded ecosystems, including oceanic islands (Hansen *et al.* 2002, Dupont *et al.* 2004). Based on floral traits, such as a slightly tubular corolla with readily accessible nectar, relatively high nectar sugar concentration, and modest nectar volume, we speculate that the original pollinators of *B. zaluzania* might have been flies or short-tongued solitary bees. However, fruit and seed set of *B. zaluzania* in our study was comparable to that of other closely related plant species in the same family on the Mascarene Islands (Pailler *et al.* 1998a, Pailler *et al.* 1998b). Thus, while feral honey bees may out-compete and displace native pollinators, our findings suggest that honey bees appear to be adequate pollinators of *B. zaluzania*. However, when comparing native pollinators with introduced honey bees, other aspects of pollination quality have to be accounted for, such as the abilities to maintain genetic diversity and pollen flow between populations (e.g. Paton 1993).

We found pollen grains of both experimental plant species on individual honey bees visiting *B. zaluzania* indicating that honey bees switched between visits to *B. zaluzania* and *P. cattleianum* and acted as shared pollinators. We additionally sampled 54 styles of *B. zaluzania* to explore whether the foreign pollen loads by honey bees were also reflected by the deposition of foreign pollen on the stigmas. Unfortunately, we could not identify pollen types clogging the stigmas because the pollen was highly clustered and well integrated into the stigmatic surface making identification and counting impossible. However, if *P. cattleianum* pollen clogs *B. zaluzania* stigmas, this should have been reflected in differences in fruit and seed sets between treatment and control plants. Differences in pollen loads (large amounts of *P. cattleianum* pollen on honey bees from control plants and comparatively low overall loads on honey bees from treatment plants) also suggested a certain degree of segregation in the pollinator assemblage into pollen and nectar foragers (see Wilson 1971). Butz Huryn (1997) reviewed studies on honey bee pollen loads and showed that they intensively utilise only a small proportion of plant species. She pointed out that if only small amounts of pollen are

removed, little effect on the flora can be expected. This pattern may explain the robustness of reproductive success of *B. zaluzania* to changes in its floral surroundings. Alternatively, the manipulated area of 78.5 m^2 may have been too small to reveal marked foraging changes of pollinators. Honey bees are capable of flying relatively long distances (Steffan-Dewenter & Tscharntke 1999) and, when foraging, respond to large-scale changes in habitat structure (Menzel *et al.* 1997, Steffan-Dewenter *et al.* 2002), which may account for the lack of indirect interactions via pollinators in our experiment.

Our results demonstrate that the presence of the invasive *P. cattleianum* flowers has no effect on the foraging behaviour and the efficiency of shared honey bee pollinators, and that the subsequent reproductive success of the native *B. zaluzania* is not changed for plants in close proximity *P. cattleianum* flowers. Nevertheless, it may be that honey bees have replaced the original pollinators of *B. zaluzania* and indirect effects may have occurred in the past. At present, indirect interactions between invasive *P. cattleianum* and a simultaneously flowering native plant species via pollinators do not appear to amplify the direct competitive effects of this successful invader. In conclusion, given the absence of indirect interactions mediated by shared pollinators in our study and contrasting findings from other experimental studies on single plant species, we suggest employing quantitative plant–pollinator network studies to elucidate the indirect impact of invasive plant species on the entire plant community, and thus to establish how indirect interactions contribute to the structure of flowering plant communities.

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TABLES

Table 1 Number of observed visits by different animal species. Observations were conducted for eight hours (16 half hour sessions) on treatment (*P. cattleianum* flowers removed) and control plants (unmodified). Numbers in brackets are total number of flowers observed. Mean (± SE) visitation rate (visits flowers^{-1} hour^{-1}) was calculated by using the mean visits for each observation session and plant (treatment: $n = 5$; control: $n = 6$).

	Flower visitors	No. of visits	Visitation rate
Treatment (185)	*Apis mellifera* L. (Hymenoptera)	104	0.98 ± 0.47[a]
	Pristomerus sp. (Hymenoptera)	1	0.009
	Villa unifasciata Macquart (Diptera)	3	0.021 ± 0.014
	Zosterops mauritianus Gmelin (Aves)	2	0.008
Control (163)	*Apis mellifera* L. (Hymenoptera)	66	0.63 ± 0.29[a]
	Allograpta nasuta Macquart (Diptera)	1	0.007
	Chaetocnema sp. (Coleoptera)	1	0.021
	Curculionidae (Coleoptera)	1	0.021

[a] $F_{1,9} = 0.38$, $P = 0.56$

Table 2 Comparison of floral and reproductive traits of *B. zaluzania* when flowers of *P. cattleianum* were experimentally removed (treatment) versus when *P. cattleianum* flowers were present (control).

Traits	Means ± SE		*df*	*F*	*p*
	No *P.cattleianum* flowers	With *P.cattleianum* flowers			
Buds per plant	44.8 ± 4.1	50.3 ± 5.6	1,19	0.61	0.44
Flowers per plant	1049 ± 163	979 ± 172	1,19	0.26	0.61
Inflorescences per plant	23.6 ± 3.6	19.3 ± 3.0	1,19	0.84	0.37
Fruits per plant	560 ± 116	524 ± 118	1,18	0.05	0.83
Fruit weight	0.47 ± 0.03	0.52 ± 0.02	1,18	3.86	0.06
Fruit size	9.8 ± 0.34	10.3 ± 0.23	1,18	1.58	0.22

FIGURES

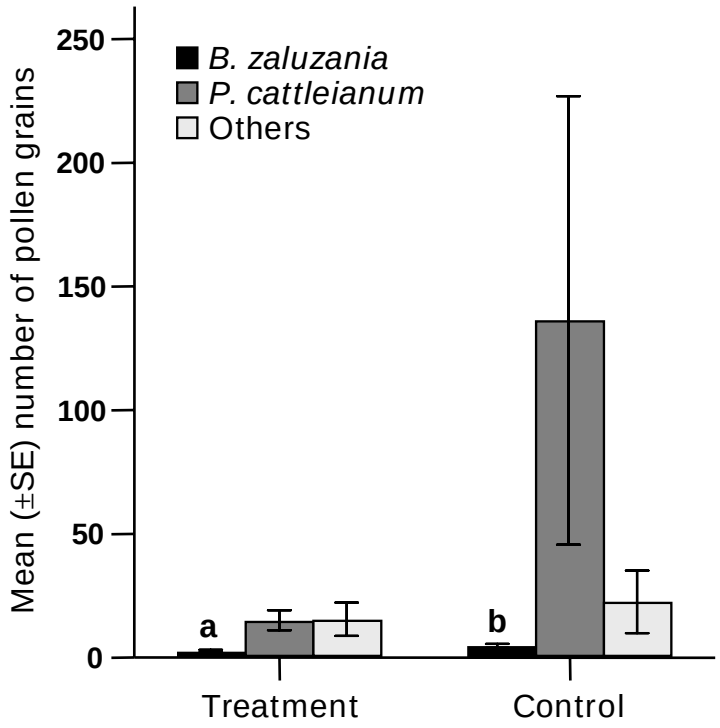

Figure 1 Mean number of pollen grains (± 1 SE) from insects that visited flowers of treatment and control plants. The pollen loads of 35 insects were collected and sorted into three groups, *Bertiera zaluzania*, *Psidium cattleianum*, and unidentified pollen (Others). Different letters on bars indicate significant differences ($P < 0.01$).

CHAPTER 5

Exotic pest insects: another perspective on coffee and conservation

Christopher N. Kaiser, Dennis M. Hansen and Christine B. Müller

(submitted to *Oryx*)

Studies in biodiversity research and conservation biology have emphasised that we should be concerned not only about the loss of species but also about the loss of ecosystem functions and resulting ecosystem services (e.g., Daily 1997). Pollination and pest control are two examples of crucial ecosystem functions and their loss may have profound ecological, economical and social consequences (Chapin et al. 2000). Animal pollination represents a critically important group of ecosystem functions, which is of particular value in agricultural landscapes (Nabhan & Buchmann 1997; Roubik 2002). For example, it is estimated that crop pollination by animals is worth $112 billion per year on average (Costanza et al. 1997). With more than 66% of the world's 1500 crop species pollinated solely by bees, the decline of managed and wild pollinating bees is therefore a concerning trend (Allen-Wardell et al. 1998; but see Ghazoul 2005). Recent research has highlighted the role of natural habitats in maintaining a high pollinator diversity that provides stable, high levels of pollination services to nearby crop plants (Roubik 2002; Klein et al. 2003; De Marco & Coelho 2004; Ricketts 2004). Similarly, the natural service provided by predatory and parasitic organisms in controlling pest species on crop plants may depend on the diversity of natural habitats, in which these organisms can persist throughout their life cycles when pest insects are not available (Naylor & Ehrlich 1997). Thus, current consensus is that the management of agricultural landscapes in the tropics should aim to maximise the benefits derived from ecosystem services rendered by animals, by maintaining structurally diverse habitats, which harbour stable populations of beneficent animal species.

One well-studied crop plant in the tropics is coffee. In many tropical montane regions, forest fragments are embedded in a matrix of traditional coffee plantations (Perfecto et al. 1996; Perfecto & Vandermeer 2002). Planting coffee bushes in proximity to forest fragments or even directly in the forest increases coffee yield because the structurally more complex habitat of the forest supports a higher diversity and abundance of pollinators and natural pest

control agents for the coffee plants than agricultural, impoverished land (Moguel & Toledo 1999; Klein et al. 2003; Ricketts 2004; Steffan-Dewenter et al. 2006).

While the benefits of native animals to crop plants in the tropics are increasingly being assessed and used to inform agricultural and related conservation policies, fewer studies are concerned with the reverse impacts from agricultural practices and introduced animals on native plants in their natural habitats. Why the disparity? The most obvious explanation is that quantifying positive effects of e.g., pollinator diversity, or negative effects due to pest species on crop yield, is more straightforward and economically rewarding than measuring gains or losses in biodiversity in the surrounding natural habitats (Edwards & Abivardi 1998). While these effects on crop yield can be expressed directly in economic terms, it is more difficult to assign a universally understandable economic value to a change in natural ecosystem functioning, which can only be assessed indirectly following a decrease of biodiversity in natural habitats (Pearce 2001).

One potential negative consequence of mixing crop plants with natural habitats, apart from the obvious detrimental effects of habitat fragmentation and loss in the first place, could be the invasion of pest species from agricultural landscapes to the surrounding, embedded natural habitats. Certainly, the global distribution of many crop species provides a large base for invasion of pest species from agricultural landscapes to surrounding natural habitats (see Mack et al. 2000). Wild hosts can provide an opportunity for pest species to build up or maintain reservoir populations before dispersing to cultivated hosts (Panizzi 1997; Sudbrink et al. 1998; Fox & Dosdall 2003), but the role of wild hosts in pest population dynamics is usually only considered when there is an economic impact on crop yield (van Emden 1981). Although such research bias is inevitable, it is vital to also consider the opposite view that crop plants can serve as hosts from which pests may spread into natural habitats.

Here, we add another perspective to the present debate on coffee and conservation in the tropics by presenting an example from the island of Mauritius, where an introduced coffee pest species wreaks havoc on the reproductive success of an endangered endemic plant. In Mauritius, commercial coffee *Coffea arabica* L. (Rubiaceae) plantations were established in 1721 (Rouillard & Guého 1999). The coffee berry moth *Prophantis smaragdina* (Lepidoptera; Crambidae) was accidentally introduced to Mauritius and was first documented in 1938 (Vinson 1938). It has long been recorded on *C. arabica* in other countries, for example on the island of Sao Tomé where it destroyed up to 80% of the coffee yield (Derron 1977). The last reported infestation of *P. smaragdina* on coffee in Mauritius was in 1995 on plantations close to the Black River Gorges National Park, which contains the largest remaining area of native

forest on the island. Preliminary observations in the National Park during another experimental study (Kaiser 2006) suggested a strong negative effect of herbivory by *P. smaragdina* on the fruit production of the endemic dioecious plant *Bertiera zaluzania* (Rubiaceae). To substantiate these observations, we monitored the fruit development of 20 randomly chosen female *B. zaluzania* plants in a population on Plaine Champagne, an upland heath area within the National Park. We surveyed 10 randomly selected infructescences per plant in the first week of February 2004 and 2005, once their fruits had started to develop and had reached a size of approximately 4 mm in diameter. In 2004, 14 out of 19 plants (flowers of one out of the 20 randomly chosen plants were attacked by fungi and did not set any fruit) were attacked by *P. smaragdina* caterpillars (Fig. 1a), affecting an average of 23.0% (SD ± 19.6) of infructescences in attacked plants. Within two weeks, all fruits on attacked infructescences were destroyed (Fig. 1b). In 2005, all 20 experimental plants were attacked, at a mean rate 81.3% (SD ± 21.2) infructescences per plant. This represented an increase in individual attack rate from 73.7% to 100%, and a three-fold increase in attack rate of infructescences per affected plant, compared to 2004. It is unlikely that *B. zaluzania* is the only endemic Mauritian Rubiaceae affected by this pest species, but no surveys have been carried out for any other species in the family. As in many tropical countries, the Rubiaceae is species-rich in Mauritius, where 15 genera and 59 native species occur, 88% of which are endemic to the island. Twenty-nine of these species are listed as endangered or critically endangered according to IUCN criteria (Mauritian Wildlife Foundation, unpublished database). Given that the National Park is surrounded by crops and plantations of exotic species, it is likely that associated pest species will utilise new host species among native plants in the vicinity. This may pose an additional significant threat to the critically endangered Mauritian flora and further research on this issue is needed.

Our observations from Mauritius are applicable elsewhere. In North Queensland, Australia, Blanche et al. (2002) compiled information on 49 economically important arthropod pest species, of which 31 (63%) were introduced. Nine of these species used native rainforest host plant species for at least part of their life cycle, and the author emphasized that planting crops close to the forest might not be wise.

In conclusion, we highlight the potential importance of a neglected area of agro-environmental research. It is ironic that, although these schemes are intended to both benefit from and protect areas of native habitat, they may in fact accelerate the impoverishment of such areas, and thereby ultimately compromise their own existence. Studies into such contrary

effects are urgently required to counteract the largely one-sided economical approach which has dominated this emerging and active field of research to date.

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FIGURE

Figure 1 Fruit stands of *Bertiera zaluzania* (Rubiaceae) (a) freshly attacked and (b) fully destroyed by *Prophantis smaragdina* (Lepidoptera; Crambidae). Once the developing fruits showed signs of attack, all fruits of a fruit stand were destroyed after two weeks.

CHAPTER 6

Visitation webs of plant–pollinator communities in restored and unrestored Mauritian heathland habitats[1]

Christopher N. Kaiser, Jane Memmott and Christine B. Müller

ABSTRACT

Little is known about the effects of introduced species, or the removal of invasive plant species for habitat restoration, on native mutualistic plant–pollinator interactions, despite pollination being essential for the reproduction of many plant species. We used fully quantified flower visitation webs to investigate plant–pollinator communities of a restored (no introduced plant species) and an unrestored (invaded by exotic plants) site in Mauritius. Our study had three main objectives, 1) to compare community structure of restored and unrestored sites; 2) to identify key species in the webs and 3) to estimate the potential effects of introduced species on the plant–pollinator community structure. Interactions between the majority of flowering plant species and their pollinator species were recorded for both sites (each ~3 ha) between September 2003 and March 2004. The visitation web of the restored site was almost twice as large as the web of the unrestored site, reflecting higher plant and pollinator species richness and abundance in the former site. Plant species in the restored site produced larger and heavier fruits, which contained more seeds per fruit than those in the unrestored site. Vertebrate pollinators were rare in the unrestored site, but relatively abundant and highly linked in the restored site. Visitation webs in both sites were dominated by a few super-abundant, disproportionately well-connected plant and pollinator species, and many rare and specialised species. The majority of mutualistic interactions at each site was asymmetrical. Key plant species at both sites were native to Mauritius, in contrast to key animal species, many of which were introduced. Differences in plant community structure between the sites appeared to have strong effects on the associated pollinator community and their interactions with native plant species. Introduced plant species produced a high fruit set, despite being visited by relatively few pollinators. Overall, our results indicated that the community structure was more complex in the restored than in the unrestored site. The web of

[1] Parts of this chapter will be written as manuscripts for three publications, each dealing with one of the three main objectives of this chapter. To avoid repetition, we combined these manuscripts in one chapter

the restored site showed higher plant linkage and pollinator diversity and abundance, suggesting habitat restoration may be crucial for maintaining functional ecosystem integrity. The dominance of a few super-abundant, super-generalist species may be critical, irrespective of their origin, for ecosystem stability and to ensure reproductive success of a wide range of native plant species. Our findings indicate that the effect of introduced species on plant–pollinator interactions may differ according to whether they are plants or pollinators. The low visitation rate to introduced plant species suggested a low level of indirect competition for pollinators with native plant species. However, the infiltration of the local pollinator community by introduced flower visitors suggested strong competition between native and introduced pollinators for floral resources, which may have resulted in the displacement of native pollinators and consequently the disruption of co-evolved plant–pollinator interactions. For habitat restoration to be successful in the long-term, practitioners should maintain structural diversity to support a species-rich and abundant pollinator assemblage which ensures native plant reproduction.

INTRODUCTION

The majority of flowering plant species rely on interactions with pollinators for reproduction (Buchmann & Nabhan 1996). Flower visitors benefit from these interactions, for example by obtaining food in the form of pollen or nectar (Proctor *et al.* 1996). Such mutualistic relationships are widely acknowledged to play a central role in the diversification of life (e.g. Baker 1963, Thompson 1994). Initially, specialisation was thought to be the dominant evolutionary trend driving this diversification within pollination systems (Faegri & van der Pijl 1979, Armbruster *et al.* 2000). Indeed, as early as 1862, Darwin suggested that the interaction between a long-spurred orchid species and a highly specialised pollinator species may have led to the evolution of the peculiar flower morphology of the orchid. More recently, the role and extent of specialisation in pollination systems have been questioned. On a community level, where many flowering plant species interact with a range of pollinator taxa, it is generalisation that appears to emerge as the predominant pattern in pollination systems (Moldenke 1975, Herrera 1987, 1988, Waser *et al.* 1996).

Numerous authors have highlighted the need to understand these mutualistic processes on the community level (e.g. Petanidou & Ellis 1996, Kearns *et al.* 1998, Memmott 1999) because surveying only a sample of plant–animal interactions within a community may bias our conceptual understanding of pollination systems. Community-wide patterns in plant–pollinator networks can be explored through the application of a food web approach (Memmott 1999, Dicks *et al.* 2002, Olesen & Jordano 2002). Evolutionary ecologists have frequently assumed that interaction partners are equally (symmetrically) specialised but, by using a food web approach, asymmetrical specialisation (non-reciprocal specialisation) was shown to be more common than was previously thought (Vazquez & Aizen 2004, 2006). For example, an individual plant species may depend strongly on a particular pollinator species, but this pollinator might utilise many plant species, and therefore show only a weak dependence on the plant species in question. Such asymmetry can only be revealed by applying a community-based approach such as food web analysis. Community-level studies can also provide important information on ecosystem stability (Bascompte *et al.* 2006), the consequences of disturbance (e.g. extinctions; Memmott *et al.* 2004), and restoration of degraded ecosystems (Hobbs & Norton 1996, Montalvo *et al.* 1997).

While food webs describe patterns of flow of energy and materials resulting from feeding relations, e.g. predation of organisms in natural communities (Cohen *et al.* 1993), the basic theoretical concepts can also be applied to networks of mutualistic interactions, such as pollination (Jordano 1987, Fonseca & Ganade 1996). Community structure can be

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characterised by the analyses of pollination networks, which employ several standard food web statistics such as linkage (Paine 1980, Pimm 1980) and connectance (Martinez 1992). Linkage describes the number of links per species, where a link is an interaction between a pair of mutualistic partners. Connectance is defined as the fraction of observed interactions over the total number of possible interactions. Visualisation of the network structure in flower visitation webs, like food webs, can also be a powerful tool. Visitation webs provide complex yet tractable depictions of species richness and evenness (relative abundance), interaction frequency, and ecosystem structure and function. For example, quantitative information on visitation frequency provide some measure of reliance of the pollinator on the plant or vice versa (Jordano 1987, Laska & Wootton 1998). Visitation webs indicate this information by depicting the fraction of an animal's species visits to a plant species in relation to its total number of visits to all species in the community.

Despite recent advances in the field of visitation web analysis, most community studies are confined to temperate, arctic or high altitude habitats, largely due to practical constraints. Tropical and subtropical plant–pollinator communities are often extremely species-rich, and as a result, studies on entire assemblages may face insurmountable obstacles. Consequently, to date, most pollination studies in diverse ecosystems have focused on subsets of entire communities such as taxonomic groups of pollinators or phenologically or spatially restricted plant species (e.g. Ramirez 1989, Kanstrup & Olesen 2000, Kato & Kawakita 2004). A few comprehensive studies have compiled data on the reproductive biology of most flowering plant species within a tropical or subtropical forest community (Percival 1974, Kato 1996, Momose *et al.* 1998). However, despite the large efforts that went into collecting these data, the studies primarily report "qualitative" information on species diversity, community composition and flowering phenology. To explore mutualistic webs with a food web approach, quantitative data on interaction frequency within well-defined spatial boundaries of the study site is required. In this study, we present two fully quantified visitation webs of entire flowering plant communities on the oceanic island of Mauritius.

Island ecosystems have undergone multiple plant and animal extinctions (Simberloff & Boecklen 1991). In contrast to the proposed balance between species immigration and extinction on islands by the equilibrium theory of island biogeography (MacArthur & Wilson 1967), the current extinction rate of island species vastly exceeds the natural fluctuations of extinction rates (Whittaker 1998). Many of the drivers of this extinctions are ultimately human-caused, such as habitat fragmentation and degradation (Bolger *et al.* 1991), exploitation of natural resources (Rainbird 2002, Mauremootoo *et al.* in press-a) and the

intentional or accidental introduction of alien plant and animal species (Moulton & Pimm 1986, Vitousek *et al.* 1997, Mack *et al.* 2000). Islands are particularly prone to species invasion (e.g. Simberloff 1986, Lonsdale 1999), and the consequences for native communities are often detrimental. Mutualistic associations, such as in plant–pollinator interactions, are likely to be impaired by the loss of biodiversity due to species invasion (Kearns *et al.* 1998, Traveset & Richardson 2006). Cox & Elmqvist (2000) reviewed the loss of pollinator species on Pacific Ocean Islands, which can either reduce plant reproductive success (e.g. Jennersten 1988) or result in a complete breakdown of breeding systems (e.g. Washitani 1996). However, despite the evidence that invasive species degrade ecosystems, resulting in changes to the structure and the functioning of the system (Naeem *et al.* 1994, Cronk & Fuller 1995, D'Antonio & Dudley 1995, Callaway *et al.* 2004), the actual impact of invasive species on ecosystem functions remains elusive.

Quantified visitation webs are ideal tools for understanding invasion processes on the community level. Plant–pollinator interactions do not occur in an "ecological vacuum" (Jordano *et al.* 2006), and shifts in interaction frequency or pair-wise dependency caused by the arrival of alien species may be best understood within the wider network of interactions. On a community level, the loss of single, generalist pollinator species may not be critical because other generalist pollinators can replace lost species. However, on a larger scale, a pool of diverse generalist pollinator species is essential to minimise any negative effects caused by temporal or spatial fluctuations in pollinator abundance (Fishbein & Venable 1996, Kandori 2002). A few studies have applied a community-wide approach to explore the impact of introduced species on native mutualistic associations (see Memmott & Waser 2002, Olesen *et al.* 2002, Morales & Aizen 2006) and have used a fully quantified approach to explore community-wide patterns of plant and animal invasion (Schönrogge & Crawley 2000, Henneman & Memmott 2001, Olesen *et al.* 2002).

Native species which contribute disproportionately to the network of interactions in the community by either showing a high visitation frequency or interacting with many plant species may rarely be replaced by another native or introduced species in the community. We define key species as extremely abundant, generalist species with an exceptionally high number of interactions with other species. Such key species are essential in maintaining ecosystem functioning, especially when they are critical to mutualistic relationships (Chapin *et al.* 2000). In plant–pollinator systems, the community role of species is difficult to assess since community-wide experimental studies on interaction strength are unfeasible. However, it is possible to identify key species by addressing species abundance, interaction frequency,

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the number of interaction partners (super-generalist, *sensu* Olesen *et al.* 2002), and the degree of mutualistic dependence between plants and their pollinators on a community level (Bascompte *et al.* 2006). Such measures can also be used to predict the consequences of the loss of key species for mutualistic relationships in the communities.

The loss of forests and the decline of native biodiversity in Mauritius are well documented (e.g. Vaughan & Wiehe 1937, Cheke 1987a) and only about 2% of the island is covered with some degree (>50%) of native forests (Mauremootoo *et al.* in press-b). *In situ* restoration of degraded habitat in Mauritius consists primarily of hand-weeding introduced plant species in small areas of a range of habitat types, from which introduced grazers like Javan deer *Cervus javanicus* and pigs *Sus scrofa* are excluded with fences. These efforts have resulted in a gradual regeneration of native flora within restored plots (Mauremootoo *et al.* in press-c). Unfortunately, there is little information on whether by restoring the native flora, the native, co-adapted animals re-colonise these areas and fulfil their previous ecosystem functions. To address this problem, we compile quantified flower visitation webs of two communities, one managed site where restoration is in progress and where weeding of all introduced plant species was initiated in 1996, and one heavily degraded, unrestored site.

To increase the success of habitat restoration programmes, Hobbs and Norton (1996, see also Montalvo *et al.* 1997) developed some general guidelines, which, when followed closely, increase the long-term viability and credibility of restoration efforts. One key issue is the understanding of basic biological and ecological processes that operate at restoration sites. In Mauritius, basic information on invertebrate diversity and abundance is rudimentary, and the understanding of key ecosystem processes is poor so ecosystem integrity during or following habitat restoration programmes has not yet been investigated.

Our study has three main objectives; namely 1) to investigate plant–pollinator community structure; 2) to identify key species and; 3) to estimate possible effects of introduced species on the plant–pollinator community structure. We compare an area of restored native habitat with a similar unrestored and degraded area and use the findings to suggest guidelines for habitat restoration. Specifically, we address the following questions:

1) What is the structure of plant–pollinator communities in the restored and unrestored habitat? Parametres such as soil nutrients, micro-climate, relative plant and flower abundance, fruit traits, and abundance and diversity of flower visitors serve as ecological indicators of restoration-induced differences between sites.
2) Can we identify species with disproportionally large impacts on the plant–pollinator communities? Given that the importance of individual species, or

species pairs in the case of mutualistic interactions, can vary across communities (e.g. Berlow 1999), we identify key plant and animal species in both sites. Since the loss of animal key species may result in a rapid decline of plant species (Memmott *et al.* 2004) these are important in habitat restoration schemes (Mills *et al.* 1993). More specifically, we ask: how generalised is each community, and is asymmetrical specialisation common on the species and the community level?

3) What is the contribution of introduced animal species to the pollinator communities of restored and unrestored habitats and what is their potential role as pollinators to native plant species? We use highly resolved subsets of visitation webs that are taxonomically split into different groups of pollinators. Such taxonomical splitting allows us deeper insight into the relationships between native and introduced plant and animal species.

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MATERIALS AND METHODS

Study area and sites

The Black River Gorges National Park in the south-east of Mauritius (20°42' S, 57°44' E) encompasses an area of 6754 ha (Fig. 1a). The area comprises the last remnants of upland moist forest, a formerly widespread plant community with several intergrading vegetation types, including *Erica/Phylica*-heath vegetation (Vaughan & Wiehe 1937, Strahm 1994). This unique vegetation type is characterised by plants growing on relatively unweathered lava with, in places, a shallow layer of soil. In Mauritius, it now occurs in only a small area of < 0.8 km^2 at Plaine Champagne and Pétrin, since in the 1970s, large areas of this native habitat were drained, clear-cut and replanted with *Pinus* sp (Cheke 1987a). The two xeromorphic shrubs *Erica brachyphylla* (Benth.) Oliv. (Ericaceae) and *Phylica indica* E. Mey. (Rhamnaceae) dominate in areas where top soil is virtually absent, and plants often experience physiological drought despite a mean annual rainfall of 4500–6000 mm and a mean monthly relative humidity of 88–96% (Mauritius Meteorological Service, 1991 – 2002). In lower areas of the habitat where soil accumulates and water run-off is reduced, the heath gives way to dwarf forest with two prominent strata; a shrub strata characterised by a great diversity of woody flowering plant species and orchids (>150 spp.; Strahm 1994) forms a layer of 1–4 m in height, and a higher canopy layer at 4–6 m height of stunted *Sideroxylon cinereum* Lam.*, S. puberulum* DC. (Sapotaceae) and *Calophyllum eputamen* Stevens (Guttiferae) trees, which emerges above the scrub layer. Overall, the habitat is a mixture of relatively open areas with almost no herbaceous layer and interspersed patches of dense, thicket-like vegetation formed by several woody flowering plant species (see Appendix II).

Since 1986, the governmental National Parks and Conservation Service (NPCS; before 1996 part of the Forestry Department) and the Mauritian Wildlife Foundation (non-governmental organisation; MWF) have established 10 Conservation Management Areas (CMAs; total area 44 ha) across all major habitat types to restore small areas of native flora. Each CMA is fenced and introduced plants are hand-weeded twice a year. The disparate native flora makes a comparison of the flower visitor communities among vegetation types ecologically unsuitable. We chose two study sites, one restored and one unrestored, within an area of one vegetation type.

The restored study site was Pétrin CMA (Figure 1b; 6.2 ha), which was fenced and initially weeded in 1994 (Mauremootoo *et al.* in press-c). Pétrin CMA represents the last sample of restored heath community in Mauritius, which has been described as the "most

striking associes of the uplands" by Vaughan & Wiehe (1937, p. 305). We will use the term 'restored site' to describe the CMA.

The second study site of equal size and with similar plant community characteristics to the CMA but in an unmanaged area, hereafter referred to as 'unrestored site', was set up at a distance >500 m from the restored site. The major difference between the restored and the unrestored plant communities was the dominance of invasive alien plants in the unrestored area. In parts, Strawberry Guava *Psidium cattleianum* formed a virtually continuous, almost monospecific stand with a maximum height of 1–1.5 m depriving the unrestored heath community of the characteristic open structure visible in the restored site. In places where soil is practically absent, other invasive introduced species such as *Wikstroemia indica, Ardisia crenata* and several herbaceous Melastomataceae species root in the crevices between the volcanic rocks. In addition to being strong competitors for nutrients and light, the dominance of introduced plant species in the unrestored area poses a serious threat to native plant species due to competition for water, particularly during the flowering season, which overlaps with the dry season. We also selected the unrestored site based on three further criteria; (1) it represented a homogeneous heath community with floral species diversity similar to that of the restored site; (2) it used to belong to the same continuous habitat type; (3) the distance of ~500 m between the restored and the unrestored site was considered large enough for their pollinator communities to be largely independent (although it is possible that long-distance foragers such as birds and large bees crossed the area between the two sites; see Fig. 1b).

In both study sites, we marked out a rectangular study area (330 × 100 m) in which we set up 23 parallel 100 m transect, at intervals of 15 m (Fig. 1b). Transects were divided into five 20 m sections. Thus, each section was 15 m wide (7.5 m on either side) × 20 m long. This grid allowed us to conduct stratified random sampling of flower and fruit abundance estimates of the plant community (further explanations in section '*Plant communities*').

Pétrin CMA borders exotic pine plantation and a dirt road on one side and heavily degraded heath community with a similar native plant species to the restored site on the other three sides, whereas the unrestored site is surrounded by similar homogenous degraded habitat on all sides.

Soil and climate

To compare differences in soil composition and nutrient content between the two sites, we collected soil from each area. Along six transects evenly spread over the study site (i.e. transects 2, 6, 10, 15, 19, and 23) we gathered topsoil every 5 m and pooled it to obtain one

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sample per transect. The soil samples were analysed for humus, clay and silt (in %), pH, salinity (mg/100g), nitrate, phosphorous, potassium, calcium and magnesium (all mg/kg; soil analysis Schweizer/Samen AG, Thun, Switzerland).

At Pétrin, September to November are dry and warm months (monthly mean ± SD; 135.5 ± 24.5 mm rainfall, 18.4 ± 1.6 °C temperature) and from December to March it is moist and hot (394.3 ± 85.6 mm rainfall, 22.3 ± 0.8 °C temperature; Mauritius Meteorological Service, 1991 – 2002). Due to regular weeding of introduced plants in the restored site, little shelter is provided by ground vegetation to protect the woody flowering plants from dehydration, particularly during the dry season. Insect behaviour is also likely to be affected by local differences in physical factors such as temperature and humidity. We measured temperature (in °C) and relative humidity (in %) from 15th December 2003 to 23rd March 2004 in each observation session (n = 455). The measurements were recorded close to the ground underneath the observed plant, and we took the mean of two readings at the beginning and the end of the observation session.

Community structure

Plant communities

To determine plant species abundance, we surveyed the plant communities of the restored and the unrestored site in March 2003 by recording every plant individual of all flowering plant species along transects. We concentrated on woody plants; a few species of herbaceous native plants and all epihytic orchids were excluded from the survey. Due to the semi-continuous stands of *P. cattleianum* plants in the unrestored site, we counted the number of individuals over 30 cm in height in 10 random 1 m^2 plots along each transect. The number of individual plants per transect was multiplied by the area per transect (1500 m^2) to calculate total abundance of *P. cattleianum* in the unrestored site.

To produce a quantitative measure of flower density over time at each study site, we conducted fortnightly flower counts, starting in calendar week 37 (15th September 2003) and finishing in week 9 (15th March 2004). Counts were always carried out at the beginning of each fortnight. We counted the number of floral units in a total of 230 cubic metres for each site. One floral unit was defined as a group of individual flowers that could be regarded as a composite flower. The mean number of flowers per floral unit for each species was calculated by averaging the number of flowers from 20 randomly selected floral units from different individuals per plant species. Only four plant species included in this study displayed multiple open flowers per floral unit (*Flagellaria indica* L., Flagellariaceae, mean flowers per floral

unit = 12.0; *Stillingia lineata* ssp. *lineata* Müll. Arg., Euphorbiaceae, 11.0; *Helichrysum proteoides* Baker, 3.9; *Psiadia terebinthina* Scott, both Asteraceae, 4.0), and hereafter we use 'flowers' and 'floral unit' interchangeably.

Two metre cubes (3-dimensional quadrats) were placed randomly (alternating left and right) within each 20 m transect section. A random number (1 – 10) defined the distance in number of steps between the start of the transect section and the first cube, and the first cube and the second cube for a given fortnightly count. Transects were walked alternately up and down and the direction was changed every fortnight. Plants within 2.5 m on either side of the transect were included in the flower counts. Due to the rarity of some plant species in the study sites, not all plant species were represented by random counts along the transects. To compare floral abundance between sites, we counted the number of flowers per cube on one flowering individual each fortnight and took the average of those readings as a measure of floral abundance for five species in the restored and seven species in the unrestored site. Floral abundance (*f*) was calculated by dividing the total number of floral units for each species counted during the sampling season by the total number of cubes sampled for each site ($n = 3450$). Thus, the floral abundance of a plant species is defined as the mean number of flowers per cubic meter.

In addition to flower counts, we also noted the number of ripe and unripe fruits per cube to obtain a quantified measure of reproductive success for each plant species. Fruit abundance was similarly calculated by dividing the total number of ripe and unripe fruits by the total number of sampled cubes. In pollination studies, plant reproductive success is conventionally expressed as fruit set, which is the proportion of flowers that set fruit. In a community study with 87 plant species, marking individuals of most plant species and recording the number of flowers and fruits is unfeasible. Therefore, we derived a measure of reproductive success from the fortnightly fruit counts. Abundance of ripe fruits was recorded from 28 and 26 plant species in the restored and the unrestored site, respectively, and divided by the species' floral abundance *f*. We obtained an indirect measure of fruit set, which was defined as the proportion of floral units per cube that set ripe fruit. To investigate potential differences in plant reproductive performance between the two sites, we also collected ripe fruits from 15 common plant species. Seed size is an important life history trait in plants (Harper *et al.* 1970). However, in our study seed size was often too small to be measured under field conditions, or fruits had little pulp so seeds often filled a fruit almost entirely. Thus, we measured mean fruit weight (in g) and fruit size (in mm; either widest diameter or maximum length depending on the shape of the fruit of each species) and recorded the

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number of seeds per fruit for species with >2 seeds/fruit to obtain a mean number of seeds/fruit.

Mauritius lies within the inter-tropical zone with frequent cyclonic weather bringing heavy rains and severe storms between November and May. Cyclones can have serious effects on the vegetation and reproductive seasons (Cox & Elmqvist 2000, MacDonald & van Wilgen 2002). Cyclonic weather interrupts the flowering abruptly, and is more likely to occur later in the flowering season. Thus, it may be advantageous for animal pollinated plants to flower earlier rather than later in the main flowering season. The fortnightly flower counts also provided data on flowering phenology which was used to determine differences in flowering times between the two sites. We determined the beginning and the end of the flowering season for the same 50 plant species in the restored and the unrestored area. We calculated the difference in the start of flowering (taken in fortnightly periods using the beginning of flowering in the restored site as a reference) for each plant species. For example, *Stillingia lineata* began flowering two fortnights earlier in the restored compared to the unrestored site, so the difference was recorded as –2. The duration of the flowering season, interrupted or continuous, was calculated in weeks and compared between the two sites for each species.

To assess the amount of nectar offered by plant species to visitors, we collected nectar samples for all plant species. Samples were collected with 5 µl microcapillary tubes from freshly opened flowers on 2–3 plants between 6 am and 10 am (for plant species with nocturnal anthesis between 7 pm and 9 pm) and sugar concentration was measured with a hand-held refractometer (Eclipse 45–81, Bellingham & Stanley). Where no nectar was detected with the microcapillary tubes, flowers were examined with a magnifying glass to check for small amounts of nectar.

Pollinator communities

Plant–animal interactions were recorded for all plant species which flowered between the 15th September 2003 and 15th March 2004. In each fortnightly period, we identified plant species, which were either flowering or were expected to begin flowering within the next week, based on the fortnightly flower counts described in the above section. For every flowering species identified, pollinator observations were conducted for four 30 min observation sessions, totalling 2 hours of observation per species during the following fortnightly period. This approach allowed us to directly compare visitation frequency between plant species within each period. We observed pollinators for a total of 471 hours in the restored and 387.5 hours

in the unrestored site. Over the entire season, however, plant species flowered for different lengths of time. To adjust for the resulting differences in observation time among plant species, we standardised visitation observations by calculating visitation rate (v) as the number of visits per hour divided by the number of flowers observed. Whenever possible, depending on the plant abundance and the spatial arrangement of a species in the area, we observed flowers on four different flowering individuals of each species, which were evenly distributed over the study site. Observation sessions on the same species were carried out over several days and at different times of the day, if the species flowered for several days. Flower visitors were observed only during dry conditions. However, during the wet season (November–April) heavy showers frequently interrupted observation sessions, which were then suspended and continued about 30 min after the rain stopped to allow sufficient time for potential pollinators to re-emerge. During light rain or mist when visitors were scarce, observations were carried out only if necessary. We conducted pollinator observations during daylight from 6 am – 6 pm. Eight plant species in the restored and five plant species in the unrestored site (mainly Rubiaceae) were identified as potentially attracting nocturnal pollinators such a Microlepidoptera or hawkmoths. Those species were observed for one hour during the day and one hour during night (from 8 pm – 12 pm). For night-time observations, we used head-lights with red filters to minimise disturbance or attraction to potential pollinators (Kearns & Inouye 1993). It is possible that bat pollination occurred during the night for a few plant species but bats were never observed to visit flowers in Pétrin and, thus, were not included in this study.

We recorded the identity of all flower visitors which touched the sexual parts of flowers and which therefore potentially contributed to the pollination. Here, we use the terms "flower visitor" and "pollinator" synonymously. We took the number of insect individuals visiting plant species at any time during the flowering season as an estimate of insect-pollinator abundance at each site. Each visitor approaching a flowering plant was considered a new individual and was thus recorded as a new visit. An "interaction" was defined as a link between a plant and an animal species, while "visit" described a link between an individual plant/flower and an animal. We recorded the number of flowers observed and the number of visits by each pollinator. Pollinators were collected from flowers for later identification when identification by sight alone was not possible, and a morphospecies code was assigned to the animal. Subsequent visits by the same morphospecies were recorded by using the animal code, and final species identification was carried out in the laboratory. In general, birds, geckos and butterflies could be reliably identified in the field by using field guides (e.g.

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Williams 1989). Other insects were identified to species or genus level by taxonomists at various institutions (Diptera: J. C. Deeming, National Museum of Wales; Coleoptera, except Cerambycidae: B. Levey, National Museum of Wales; Cerambycidae: K. Adlbauer, Landesmuseum Joanneum Graz; Collitidae: N. Springate, Natural History Museum London; Parasitic Hymenoptera: D. Quicke, Imperial College Silwood Park, Ascot; Microlepidoptera: D. Slade, National Museum of Wales; Microlepidoptera: W. Speidel, Alexander Koenig Research Institute and Museum of Zoology, Bonn; Macrolepidoptera: S. Couteyen, Réunion; Macrolepidoptera, Sphingidae, Hemiptera: J. Williams and S. Ganeshan, Mauritius Sugar Industry Research Institute MSIRI). Approximately 50% of species could be reliably identified to species level.

To compare animal species richness of the restored site with the flower visitor assemblage of the unrestored site, we calculated sample-based species rarefaction curves. Rarefaction curves, formerly also called "smoothed" species accumulation curves (Colwell & Coddington 1994), are produced by repeatedly re-sampling the pool of *n* samples, at random, and plotting the average number of species represented by 1, 2,…., *n* samples (Gotelli & Colwell 2001). We used the ACE estimator computed by the free software package *EstimateS* (Colwell 2000) to compare the rarefaction curves of the restored and the unrestored sites. We calculated the 95% confidence interval of the difference $D = |m_{rest} - m_{unrest}|$ (*m* is the average number of species represented by 1, 2,…., *n* samples) between the two distributions according to Sokal & Rohlf (1995):

$$P\left\{D - 1.96\sigma_D \le \delta \ge D + 1.96\sigma_D\right\} = 0.95 \qquad \textbf{(1)}$$

where *P* is the probability (here 0.95) that the overall mean of the difference (δ) lies within the sample difference $D \pm 1.96$ standard deviations (σ) of the difference. That is, the two curves are significantly different from each other at the $p < 0.05$ level when they do not overlap with $D \pm 1.96\ \sigma_D$. Since we are comparing the curves and not the final species estimators, the comparison is legitimate despite not reaching a plateau, which is a common phenomenon when sampling tropical or arthropod communities (Gotelli & Colwell 2001). However, rarefaction curves can not be used for extrapolation to obtain estimates on total species richness (Tipper 1979), and non-parametric estimators should be used instead to reveal idiosyncratic differences in species richness between sampling sites (Colwell & Coddington 1994). We employed the abundance-based richness estimator ACE, which, in contrast to incidence estimators, accounts for the relative abundance of species observed (Chazdon *et al.* 1998). The ACE estimator is calculated based on the proportion of singletons (species

represented by a single individuals) and doubletons (species represented by two individuals) in the observed data, so the larger the number of singletons in a sample, the greater the difference between the observed and the true species richness. It therefore provides a reliable estimate particularly in diverse assemblages or when sampling effort may have biased observed species richness (Colwell & Coddington 1994, Chazdon *et al.* 1998).

Visitation webs

We define a visitation network as a quantified plant × animal interaction matrix describing trophic and reproductive interactions between groups of flowering plant species and their visitors within a well-defined area (*sensu* Olesen & Jordano 2002). Visitation networks are commonly illustrated as either rectangular matrices or as bi-partite visitation graphs (see Jordano *et al.* 2006). The latter consists of a set of graph vertices (in our case plant and animal species) decomposed into two disjoint sets (plants and visitors) such that no two vertices within the same set are adjacent. In such a visitation web, a line between two vertices represents an interaction between the animal and the plant species. Quantified visitation webs take account of the abundance of flowers and animals in the community, which corresponds with the size of a vertex depending on whether it represents a plant or a visitor species.

In this study, we combined two different sampling techniques. Floral abundance data were collected following a stratified sampling scheme along transects, and data on flower visitation were obtained with local observations. To adjust the data from the two sampling techniques and to scale the variables to the community level for visual and analytical presentation, we expressed the number of visits hour^{-1} flower^{-1} to a plant species as a function of its floral abundance in the study site. We defined quantified visitation rate:

$$I_{total} = \sum_{p=1}^{n}\left(\sum_{a=1}^{m}(v_a \times f_p)\right) \quad \textbf{(2)}$$

where I_{total} is the total quantified visitation rate of all animal species to all plant species, v_a is the total number of visits hour^{-1} flower^{-1} of animal species a to plant species p, and f_p is the floral abundance of the plant species p visited by a. That is, each visit was quantified based on the floral abundance of the interaction partner before summing up. We used the total number of visits of each animal species as a measure of the abundance of a visitor species. Lines representing an interaction between two vertices were drawn as wedges, and the width of a wedge represented the quantified visitation rate of the flower visitor a to the plant species p. The overall visitation webs of the entire season were drawn by a programme written in Mathematica™ (Wolfram Research, Inc., Champaign, IL, USA), and the visitation webs for

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individual insect orders were drawn by a programme written in Microsoft Visual Basics (Microsoft Corporation 2004, Redmond, WA, USA).

Structure of visitation webs

Visitation webs can be characterised by a number of parameters. We calculated the following descriptive statistics for each visitation web: (1) number of plant species (P), (2) number of flower visitor species (A), (3) species richness ($R = P + A$), (4) web size (i.e. total number of potential interactions, $S = P \times A$), (5) the total number of interactions recorded (I), and (6) the total number of visits recorded (V). We also measured network connectance, $C = 100 \times (I/S)$, which is the fraction of realised interactions in the network (Jordano 1987). During the season, network composition and size can fluctuate because plants and animals can "join" or "leave" the community, and C based on the overall community would overestimate the level of generalisation. Therefore, we calculated the overall connectance based on the mean connectance for each fortnightly period (see Medan *et al.* 2006). C is dependent on the occurrence of common, generalised and rare species. We calculated the cumulative C based on the fraction of realised interactions of 1,2,…n flower visitors to all plant species at each site. Connectance was highest when the most abundant flower visitor entered the network, and with each additional visitor species connectance decayed exponentially. Once all flower visitors had entered the network, the cumulative connectance equals the overall connectance C. We divided flower visitors in two groups, abundant and generalist flower visitors, and rare species. Whether a flower visitor species was classed as abundant or rare was determined by fitting best fit lines for regression models on groups with different species. The slopes of their best fit lines provided information on the structure of network connectance in both sites.

Key species and generalisation

Generalisation of plants and pollinators

In addition, we determined the mean linkage (l), i.e. mean number of interactions per species, the relative linkage ($l_{rel} = l/n$) where n is the number of species in a group, and the linkage level of the most-connected animal and plant species (l_{max}). To compare linkage levels between plant and animal species, we calculated the relative linkage for animals, $l_A = l_{(animals)}/P$ and for plants $l_P = l_{(plants)}/A$. Similarly to connectance, linkage level is a measure of generalisation, but on a species level.

Asymmetrical specialisation

Asymmetry in visitation webs describes non-reciprocal dependencies between plants and their pollinators. To investigate whether the interaction partner of a pollinator or a plant species was similarly generalised/specialised, we calculated the degree of specialisation of a given species and the mean degree of specialisation of its interaction partners (*sensu* Vazquez & Simberloff 2002). Species diversity consists of the two components, species richness, i.e. the number of species, and species evenness, i.e. the relative abundance of species, and those components are analogous of niche breath measurements in plant–pollinator communities. Vazquez & Simberloff (2002) defined richness as the number of different resource items used by a given species and evenness as the relative frequency of use of the different resource type. An inherent problem of species diversity measures is its dependence on sampling effort. Goldwasser & Roughgarden (1997) simulated variation in sampling effort and found that its impact on species richness, among other community characteristics, was distant. According to the authors, species richness is underestimated if it is based on interaction records since the likelihood of observing an interaction lags behind the detection of a species. To overcome this problem, we applied a rarefaction technique (EcoSim software; Gotelli & Entsminger 2000), which accounted for biases in species richness and evenness due to differences in sampling effort (Gotelli & Graves 1996). The interaction specialisation of species i (s_i), was defined as the rarefied species richness of its interaction partner, thus, the richness of plants or pollinators interacting with a given partner served as a measure of plant–animal interaction specialisation. To test for the degree of asymmetry in interactions, we calculated the weighted mean specialisation of interaction partners (p_i). Weighted means implied that we accounted for the interaction frequency of the species. For example, a given plant species utilises two flower visitors ($s_i = 2$), but its flower visitors visit on average 6.5 plant species, so we can describe the relationship between s_i and p_i as the degree of asymmetrical specialisation between the given plant and its pollinators (for a more detailed explanation see Vazquez & Simberloff 2002). Rarefaction requires a minimum number of visits for each species, and we chose two minimum rarefaction sample sizes, 10 and 20 visits. The relationship between s_i with a sample size of 10 and s_i with a sample size of 20 was highly significant (least square regression analyses for plants and animals in both sites; all $R^2 > 0.95$, $p < 0.0001$), thus we set the minimum rarefaction sample size to 10 visits. Thirty-nine (29%) and 33 (33%) flower visitor species of the restored and the unrestored area had an abundance (i.e., number of individuals recorded visiting flowers) of more than 10, and 53 (72%) and 38 (59%) native plant species in the restored and the unrestored site, respectively, received more than 10 visits.

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The specialisation index s_i and the linkage level l are conceptually similar measures. However, the latter could be calculated for all plant and animal species (i.e. it did not require a minimal number of visits) and it facilitates the comparison with other network studies since it is a common measure of species generalisation.

Introduced species

Native and introduced pollinators

To estimate the impact of introduced flower visitors on the pollinator and plant communities in Pétrin, we categorised animal species by their origin into species which are; (1) endemic to Mauritius; (2) native to Mauritius and/or the Mascarene Archipelago; (3) either known to be introduced to Mauritius or well described cosmopolitan species, which were probably introduced at first colonisation; or (4) of unknown origin largely due to the lack of species identification. Of all animal species observed to visit flowers, 51% belonged to the last group. All birds, geckos and butterfly species are well described in the literature and could therefore be easily identified and the origin of other flower visitors was determined where possible. We used to the following sources to determine the origin of flower visitors: Diptera (Orian 1962, Crosskey *et al.* 1980), non-parasitic Hymenoptera (Williams & Ganeshan 1999; S. Ganeshan pers. comm.; Mauritius), Hemiptera (S. Ganeshan pers. comm.; Mauritius), Coleoptera (MSIRI; K. Adlbauer pers. comm.; Graz), Lepidoptera (Vinson 1938, Williams 1989; W. Speidel pers. comm.; Bonn), Formicidae (L. Lach pers. comm.; Mauritius).

Data analysis

Fruit size and weight of 15 plant species in the restored and the unrestored site were compared with Student's *t*–tests, and the number of seeds per fruit of seven plant species were analysed with non-parametric Mann–Whitney *U*–tests. To compare the overall difference in fruit traits between sites, we fitted analysis of variance models (ANOVA), with site as the explanatory variable. We controlled for plant species by testing the site effect against the site × species interaction (Pinheiro & Bates 2000).

To describe the relationship between various plant community traits in the restored and the unrestored site we fitted simple linear regression models. Abundance measures such as floral, fruit and plant abundance, and quantified visitation rate were natural log-transformed to reach normality or, if entered as explanatory variable in the model, to obtain a fit of the models, which describes best the relationship between variables. A linear mixed effects model was used: firstly, to describe the difference in the relationship of floral and plant

abundance between the restored and the unrestored site. Plant abundance was entered as the response variable, floral abundance and site as fixed effects and plant species identity as a random effect; secondly, to test whether visitation rate of a plant species is dependent on its abundance, where the visitation rate was natural (log +1)-transformed, plant abundance and site were entered as fixed effects and plant species identity was entered as random effect; and thirdly, to test whether plant species linkage was related to the total number of visits received. Site was entered as explanatory variable and to account for dependences within plant species, plant identity was included in the model as random effect. The relationship between the length and start of the flowering period and fruit set was analysed with non-parametric Spearman's rank correlation (r_s).

The effect of abundant and rare flower visitors on cumulative network connectance was analysed by comparing slopes of best fit lines with linear models. Linkage was ln-transformed to compare the mean linkage for 51 plant species between sites. The effect of population size on linkage level was investigated by fitting simple linear regression models of both sites. Linkage was natural log-transformed to reach normality.

The relationships between the degree of specialisation (s_i) of plant species and the specialisation index of their interaction partners (p_i) were investigated separately for each site using simple linear regression models. Testing for the relationship between degree of specialisation of animals and their interaction partners, we distinguished between native and introduced animals and fitted an ANCOVA model with animal origin as factor. In those generalised pollination systems where functional plant diversity is low (in contrast to species diversity) and many flower visitor can access floral resources of most plant species, pollinator behaviour may be more opportunistic than in more specialised, coevolved systems. To test this hypothesis, we investigated the relationship between the degree of specialisation of plant species and their floral abundance with simple linear regressions, for both sites. A comparison of R^2 values revealed that degree of specialisation was better explained by the logarithm of floral abundance, so we natural log-transformed floral abundance for all analyses. In addition, we used simple linear regressions to test for the relationship between s_i (and p_i) and fruit set. We used linear mixed effect models to investigate the relationship between the degree of specialisation of flower visitors and their abundance. Site was entered as fixed effect to distinguish differences between sites, and species identity was included as random variable.

Introduced plant species in the unrestored site were observed for flower visitors. To determine whether introduced plant species attract more pollinator species, we compared mean linkage levels of introduced species with native plant species. Given the difference in

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the number of introduced and native species, we randomly sampled linkage level of eight native plant species without replacement and repeated the sampling 10000 times according to the bootstrap method (Efron & Tibshirani 1998). Mean linkage level for introduced plant species was compared to the bootstrapped mean and its estimated confidence intervals of native plant species. We employed the same re-sampling method to study the difference in length of flowering time between native and introduced plant species. To test for differences between linkage of native and introduced pollinators, we ran a linear-mixed effects model with log-linkage as the response variable, Origin (native/introduced) as the explanatory variable and with Site as random effect. Lastly, connectance of native and introduced animal orders was compared by a linear model. We fitted connectance against 'origin' (native/introduced) and included 'orders' as blocking term. To account for dependences within sites, we tested origin against origin × site interaction (Pinheiro & Bates 2000). All analyses were conduced with the statistic package R 2.1.1 (R Development Core Team 2005).

RESULTS

Community structure

Visitation webs

Overall, 105 flowering plant species were recorded in the plant survey; 90 of these species occurred in the restored and 84 in the unrestored site. A total of 87 species from 37 families flowered across both sites between August 2003 and March 2004; 74 (82.2%) in the restored and 64 (76.2%) in the unrestored site, and were included in the visitation webs (Fig. 2). Fifty-one plant species (23 families) occurred at both sites (Appendix III). Thirty-three of the flowering species (37.9%) were either endangered or critically endangered following the IUCN red list criteria. Five percent of plant species in the restored and 18.8% in the unrestored (only natives 12.5%) received ≤3 visits. Eight plant species (9.5%) in the unrestored site were introduced and, although all of these species flowered during the study period, animals visited only five species (Fig. 2). The eight introduced plant species accounted for 15.4% of the total floral abundance in the unrestored site, but only 7.5% of all flower visits were observed on these species. On average there were 0.48 ± 0.19 (hereafter means ± SE unless otherwise stated) visits per flower per hour to introduced plants compared to 0.59 ± 0.11 to native plants in the unrestored site. The mean visitation rate to native plant species in the restored site was 0.70 ± 0.20 visits/flower/hour. Visitation rates of all plant species at both sites are presented in the Appendix III. All introduced species produced abundant fruits despite their relatively low visitation rate.

Overall, there were 161 animal species which visited flowers (Appendix IV) – 135 species in the restored and 100 species in the unrestored site – from 65 families within five orders of invertebrates and two orders of vertebrates (Appendix V). Seventy-four species occurred in both sites, of which 23 (31%) species were introduced (46.7% of species with identified origin). Overall, 77 species (47.8%) were observed only once or twice (restored: 61 species; unrestored: 50 species), and only 14 species were recorded on flowers more one than hundred times. Rarefied species accumulation curves indicated a significant difference in species richness between sites (Fig. 3a). However, species richness estimators suggested that species richness did not differ between sites (Fig. 3b), which is largely due to the high number of species interacting only once with observed plant species. The most species-rich group of flower visitors were the true flies (Diptera; 71 species, 44%), and within this order 26 species (36%) belonged to the families Muscidae (house flies) and Syrphidae (hover flies). Social and solitary bees, which represent a major group of flower visitors in most mainland pollinator communities and which are often described as the most efficient pollinators, were extremely species-poor in our study with only one species in the family Apidae (*Apis mellifera* L.) and one solitary species in the family Colletidae (*Paleorhiza* sp.) observed. The former was the most abundant and one of the most generalised flower visitors, and the latter was observed only once. The largest difference in number of visitor species between the restored and the unrestored site was in the Lepidoptera (30 *vs* 17 species). Dipterans were the most abundant order of flower visitors (3043 visits; 41.7% of all visits) followed by hymenopterans (excluding the ant family, Formicidae, 1428; 19.6%) and the Formicidae (1035; 14.2%). While the proportion of Diptera species compared to all species in the communities and the fraction of total visits were similar (44% *vs* 41.7%), this ratio was unbalanced in hymenopterans (9.3% *vs* 19.6%), and even more unbalanced in the Formicidae (1.9% *vs* 14.2%).

Structure of visitation webs

Visitation web properties on plant–pollinator communities in the restored and the unrestored site are presented in Table 1. Overall connectance was lower in the restored (13.2%) than in the unrestored site (15.5%). Abundant flower visitors in the restored site (22 of 135 species; 14.1%; Fig. 4) explained a larger proportion of the overall connectance (restored: 71.4%, C = 25.9; unrestored: 62.4%, C = 21.8) than in the unrestored site (28 out of 99 species, 28.3%). Thus, in the restored site, 85.9% of animal species contribute to only 28.6% of the connectance (unrestored: 71.7% *vs* 37.6%). The significantly steeper decline of connectance

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in the restored site when common species were removed from the network indicated either a generally higher degree of generalisation in the restored than in the unrestored site or the presence of super-abundant pollinator (highly connected species) in the restored site (slope $\beta_{restored} = -1.31$, $\beta_{unrestored} = -0.94$; $F = 22.74$, $p < 0.0001$). On the contrary, rare flower visitor species were more generalised in the restored than in the unrestored site ($\beta_{restored} = -0.13$, $\beta_{unrestored} = -0.16$; $F = 20.27$, $p < 0.0001$).

Plant community characteristics

Both sites were dominated by a few common plant species. In the restored area where only native plant species occur, the three most abundant flowering plant species *Antirhea borbonica* Gmel. (Rubiaceae), *Aphloia theiformis* Benn. (Flacourtiaceae) and *Gaertnera psychotrioides* Baker (Rubiaceae) accounted for 30% of all plant individuals. In the unrestored site, the most abundant plant species were the introduced *P. cattleianum* and *W. indica* which, together with the most abundant native plant species *A. borbonica*, accounted for 84.6% of all plant individuals. Introduced plants accounted for 82.8% of all plant individuals in the unrestored site (Fig. 5). Plant density in the unrestored site was 1.90 plants /m^2 compared to 0.46 plants/m^2 in the restored site. The density of native plants in the unrestored site was 0.34 plants/m^2. Plant abundance of species which occurred in both sites was significantly higher in the restored compared to the unrestored site (paired $t = 3.48$, $p = 0.001$, $df = 50$). However, floral abundance, controlled for plant abundance, was similar between sites (paired $t = 1.06$, $p = 0.29$, $df = 50$). The number of flowers in the community provided by each species (floral abundance) was dependent on the length of the flowering period of the given plant species ($F_{1,45} = 12.1$, $p < 0.0001$) and on plant species abundance ($F_{1,45} = 33.6$, $p < 0.0001$), and the slope of the linear relationship between floral and plant abundance was steeper in the unrestored site (plant abundance × site; $F_{1,45} = 3.55$, $p < 0.066$). There was a positive relationship between plant species abundance and the number of pollinator species attracted (restored $R^2 = 0.14$, $F_{1,72} = 12.09$, $p = 0.001$, slope $\beta = 0.16$; unrestored $R^2 = 0.17$, $F_{1,62} = 12.90$, $p = 0.001$, $\beta = 0.19$). Plant abundance for species which occurred in both sites was positively related to visitation rate ($F_{1,48} = 4.95$, $p = 0.031$), but there was no difference in mean visitation rate between sites ($F_{1,48} = 0.77$, $p = 0.38$). Floral abundance and the number of flowers recorded during pollinator observations were highly correlated (both sites: $r = 0.74$, $p < 0.0001$, $n_{\text{restored}} = 74$, $n_{\text{unrestored}} = 64$).

The mean length of flowering season was 9.2 ± 0.8 weeks in the restored and 9.7 ± 0.9 weeks in the unrestored site. For plant species which occurred in both sites, the mean

flowering period was 1.5 ± 0.3 weeks shorter in the unrestored compared to the restored site (t = – 2.72, p = 0.009, df = 50). The two most abundant native plant species at both sites, *A. borbonica* and *A. theiformis,* flowered throughout the entire 28-week study period (Appendix VI). There was no difference in the mean length of the flowering period between native (9.49 ± 0.9 weeks) and introduced plant species (10.8 ± 2.6; bootstrapped 95% confidence interval 6.3–13.5 weeks). However, species in the restored site started flowering significantly earlier (2.3 ± 0.3 weeks; range +4 to –16 weeks) than the same species in the unrestored site (one sample t = –3.95, p < 0.0001, df = 50). Neither the difference in the start of flowering (r_s = – 0.25, p = 0.397, n = 14), nor the length of the flowering period (r_s = –0.38, p = 0.177, n = 14) had a significant effect on fruit set.

Nectar was detected in only 31 plant species (35.6% of total flowering species), thus the majority of plant species offered pollen as the sole reward for flower visitors (Appendix III). The majority of flowering species (74.7%) produced open, cup-shaped or brush flowers, which were easily accessible to a wide range of flower visitors. The dominating petal colours were white, cream and pale pink (87.9%). The main exceptions were *Trochetia blackburniana* Bojer (Malvaceae; flower colour: red), *Syzygium mauritianum* Guého & Scott (Myrtaceae; red) and *Roussea simplex* Sm. (Rousseaceae, yellow) with showy, conspicuous, and brightly coloured flowers, which offered large amounts of nectar (Appendix IX and CD). These plant species were also among the few that were visited by vertebrate pollinators.

Plant reproductive success

To compare reproductive traits of plant species between sites, we collected fruits from a total of 15 common plant species which produced a sufficient amount of fruits to make statistical analysis meaningful. Fruit size (n = 14 species), fruit weight (n = 12) and number of seeds per fruit (n = 7) were significantly different between the restored and the unrestored site (Table 2). Individuals of eight plant species (57%) produced significantly larger fruits, and six species (50%) produced heavier fruits in the restored than in the unrestored site (Fig. 6). Where a comparison of the number of seeds per fruit was possible, 57 % of species in the restored site (4 of 7) produced significantly more seeds per fruit than individuals of the same species in the unrestored site (Appendix VII). Of those four species, two had a higher and two had a lower visitation rate in the restored site. Fruit set (number of ripe fruits per m^3 divided by floral abundance) was marginally significantly higher in the restored compared to the unrestored site (restored: 0.37 ± 0.13; unrestored: 0.21 ± 0.07; paired t = 2.08, p = 0.056, df = 14). The mean number of unripe fruits per cube divided by the floral abundance was

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significantly higher in the restored site for the same 51 plant species in both site (restored: 0.24 ± 0.11; unrestored: 0.18 ± 0.11; paired $t = 2.06$, $p = 0.045$, $df = 50$).

Soil and climate

Most soil nutrients, salinity and pH-value did not differ significantly between sites. The exception was nitrate level, which was marginally higher in the restored site (Fig. 7) suggesting that nitrates were distributed unevenly in the soil and thus they may be limited in parts of the study site. Overall, the soil content was poor in all five recorded nutrients, and the pH was mildly acidic (restored: 4.9 ± 0.1 pH; unrestored: 5.6 ± 0.4 pH). Soil humus and silt concentration were significantly higher, and clay content was marginally higher in the restored than in the unrestored site (see Fig. 7).

Mean temperature and mean relative humidity from December 2003 to March 2004 varied significantly between months, times of the day and sites (three-way interaction; Table 3). The overall mean temperature in the restored was lower than in the unrestored site (restored: 27.9 ± 0.27°C; unrestored: 28.4 ± 0.25°C), and relative humidity showed the opposite pattern (restored: 75.2 ± 1.12%; unrestored: 72.7 ± 1.27). The number of flowers visited on $n = 31$ observation days with climate measurements was independent of temperature ($F_{1,29} = 0.21$, $p = 0.89$) and humidity ($F_{1,29} = 1.28$, $p = 0.27$).

Key species and generalisation

Key animal species

Key species were defined as species which contribute disproportionally to the plant–pollinator communities by showing high abundance and linkage, i.e. species with many interactions. The honey bee (*Apis mellifera*) was overall the most abundant flower visitor in the study, accounting for 15.8% of all visits (see Fig. 2). In the restored site, honey bees and the widespread fly *Stomorhina lunata* Fabricius (Calliphoridae) were equally abundant (together 27.6% of all visits), followed by the introduced yellow-footed ant *Technomyrmex albipes* Smith (10.0%) and the native ant *Brachymyrmex* sp (8.4%; both Formicidae). The sequence of flower visitor abundance was similar in the unrestored site except that, after *A. mellifera* (19.4% of visits), the accidentally introduced flea beetle *Chaetocnema* sp. (Chrysomelidae) was the second most abundant species (16.9%) and followed by *S. lunata* (6.8%), *Brachymyrmex* sp. (5.2%), and *T. albipes* (4.6%). Honey bees interacted with 43 plant species in the restored (58.1% of all plant species) and 28 species in the unrestored site (43.8%). Of these, only three species in both sites were visited by ≤3 species, including honey bees,

suggesting that honey bees did not serve as pollinators for many specialist plant species. In both sites, the visitation rate by honey bees was independent of the floral abundance of a plant species (both variables natural log-transformed, restored: $F_{1,41} = 0.05$, $p = 0.94$; unrestored: $F_{1,26} = 0.13$, $p = 0.72$). Introduced *Chaetocnema* beetles were observed to visit 15 (20.3%) and 34 (53.6%) plant species in the restored and the unrestored site, respectively. In the restored site, only 3.7% of all visits were conducted by *Chaetocnema*, compared to 17.1% in the unrestored site. Amongst others, this species was particularly abundant on flowers of the native Euphorbiaceae *Stillingia lineata* (37.1% of all C*haetocnema* visits) and on the introduced *P. cattleianum* in the unrestored site (12.2%). Overall, the five most abundant invertebrate species accounted for 50.6% and 56.1% of all visits in the restored and the unrestored site, respectively. *Technomyrmex albipes* was the most generalised flower visitor in the restored site (45 spp, 60.8%; unrestored: 24 spp, 37.6%), and together with the other two ant species *Brachymyrmex* sp and *Pheidole megacephala* Fabricius they accounted for 19.8% of all visits (unrestored: 9.8%, see Fig. 2). Flower visitors of both vertebrate groups contributed only to 0.7% of all visits in the restored and 0.1% in the unrestored site. Nevertheless, the single gecko species in the study area *Phelsuma cepediana* Merrem visited 12 plant species (16.2%) in the restored and 3 species (4.7%) in the unrestored site. Similarly, birds visited more plant species (8 *vs* 2) in the restored than in the unrestored site. Overall, there were three plant species where vertebrates, particularly *P. cepediana*, were the sole regular flower visitors (see Fig. 2).

Generalisation of plants and pollinators

There was a positive correlation between the observed generalisation of plant species (linkage) and their quantified visitation rate, and the relationship was similar between sites ($F_{1,45} = 151.9$, $p < 0.000$; site × linkage $F_{1,45} = 0.09$, $p = 0.75$; Fig. 8). Six species (9.4%) in the unrestored site did not receive any visitors, compared to one species (1.4%) in the restored site. More species in the unrestored area were visited by < 4 visitor species (43.8%, 28 spp) compared to the restored site (14.9%, 11 spp; Fig. 9a). The number of plant species with a linkage ≥ 4 was higher in the restored than in the unrestored site. On average, plant species that occurred in both sites attracted more visitor species in the restored than in the unrestored site (restored: 11.57 ± 1.41, median = 9; unrestored: 9.15 ± 1.36, median = 5; paired $t = 2.93$, $p = 0.005$, $df = 50$). Linkage of native plant species was not significantly different to linkage of introduced plant species (native: 8.91 ± 1.2; introduced: 4.6 ± 2.3; bootstrapped 95% CI 4.25 – 14.25). Animal species that occurred in both sites had significantly higher linkage in

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the restored than in the unrestored (restored: 9.06 ± 1.16, median = 5.5; unrestored: 6.94 ± 0.92, median = 3; paired $t = 3.40$, $p = 0.001$, $df = 71$). The majority of flower visitors were observed to visit only one or two plant species (Fig. 9b). At the same time, both pollinator communities contained few super-generalist species with a linkage >20.

Asymmetrical specialisation

There was a significant negative relationship between plant species specialisation and the mean specialisation of their interaction partners (restored: $F_{1,51} = 9.18$, $p = 0.0003$; restored: $F_{1,36} = 4.14$, $p = 0.049$; Fig. 10), and this relationship was similar at both sites (restored $p_i = -0.09\ s_i + 7.22$, $R^2 = 0.15$; unrestored $p_i = -0.06\ s_i + 6.79$, $R^2 = 0.10$. Pollinator species were more generalised in the restored than in the unrestored site (s_i: 5.89 ± 0.23 *vs* 5.52 ± 0.25; $F_{1,28} = 7.24$, $p = 0.012$) and the level of generalisation (s_i) was positively related to pollinator species abundance ($F_{1,28} = 28.7$, $p < 0.0001$). The relationship between s_i and pollinator abundance showed a trend towards a steeper slope in the unrestored site (abundance × site: $F_{1,28} = 3.20$, $p = 0.084$). Overall generalisation of pollinator species was not related to the mean specialisation of plant species (restored: $F_{1,31} = 0.25$, $p = 0.39$; unrestored: $F_{1,25} = 0.46$, $p = 0.13$). However, while native pollinator species showed the no relation between generalisation level of pollinators and plants, introduced species showed a trend at both sites towards introduced generalists visiting more specialised plants (Fig. 11; specialisation × origin restored: $F_{1,31} = 1.28$, $p = 0.058$; unrestored $F_{1,25} = 3.36$, $p = 0.079$). The degree of specialisation and the mean specialisation of interaction partners were not related to fruit set in either the restored ($\boldsymbol{s_i}$: $F_{1,19} = 1.19$, $p = 0.29$; $\boldsymbol{p_i}$: $F_{1,19} = 0.26$, $p = 0.62$) or in the unrestored site ($\boldsymbol{s_i}$: $F_{1,18} = 0.17$, $p = 0.69$; $\boldsymbol{p_i}$: $F_{1,18} = 0.62$, $p = 0.44$).

Introduced species in taxonomical subsets of visitation webs

Structure of taxonomical subsets of visitation webs

Mean connectance of sites across taxonomical subsets did not differ (paired $t = 1.19$, $p = 0.27$, $df = 7$) and connectance compared between native and introduced animal subsets was also not significantly different ($F_{1,2} = 7.23$, $p = 0.12$; Table 4). Similarly, connectance differed only marginally among taxonomical subsets ($F_{7,14} = 2.74$, $p = 0.05$). Linkage of native pollinators in taxonomical subsets which occurred in both sites was significantly higher in the restored than in the unrestored site (restored: 10.2 ± 1.63; unrestored: 7.55 ± 1.27, paired $t = 2.53$, $p = 0.018$, $df = 26$). However, linkage of introduced pollinators were similar between sites (restored: 13.0 ± 2.64; unrestored: 10.5 ± 2.06, paired $t = 1.63$, $p = 0.116$, $df = 22$). The mean

linkage of native and introduced pollinators of both sites were not significantly different (restored: 8.87 ± 1.36; unrestored: 11.76 ± 2.24; $F_{1,97} = 1.12$, $p = 0.29$).

Native versus *introduced pollinators*

Of all observed pollinator species, 45 were endemic or native to Mauritius, 35 species were introduced and no origin could be determined for 81 species. The latter group accounted for only 9% of all visits, native and endemic pollinators carried out 28% of visits and introduced animals accounted for 63% of all visits.

The introduced honey bee, *A. mellifera*, was the most abundant flower visitor in the order of Hymenoptera (excluding Formicidae; Fig. 12; for native and introduced animal species subdivided by families see also Appendix V). In addition, two species of deliberately introduced (bio-control agents) Scoliidae-wasps and the Yellow Paper-wasp *Polistes hebraeus* were the only Hymenoptera species, which could reliably be identified as introduced to Mauritius. No plant species was exclusively visited by *Apis mellifera*, and those plants visited were also visited frequently by other generalist flower visitors.

In contrast to the Hymenoptera where one introduced species dominated the visitation web, the ratio of introduced vs. native flower visitors within the Diptera was more balanced (Fig. 13). Fifty-three percent of dipterans were introduced, and some of them were well-studied pest species (e.g. *Melanagromyza sojae* Zehntner, *Stomoxys calcitrans* L., *Bactrocera curcubitae* Coquillett, *Ceratitis rosa* Kratsch). Three Diptera species are probably new to the literature: *Homoneura* sp 1 & 2, and *Spilongona* sp (J. C. Deeming, pers. comm.). In the restored site, two cosmopolitan species often found in association with livestock or humans, *Stomorhina lunata* and *Musca domestica,* were extremely abundant, and the majority of their interactions (91%) were observed to the very common plant species *A. theiformis* and *P. terebinthina*. The most generalised endemic dipteran pollinator *Pachycerina crinicornis* (restored: l=35, unrestored: l= 21) utilised the same number of plant species but was only a third as abundant as *S. lunata*. The two species shared 68.7% of plant species in the restored and 59.6% in the unrestored site.

Lepidoptera was the order with the highest fraction of native species in relation to all identified species (90%; Fig. 14). Only one species, the African Cotton Leaf Worm *Spodoptera littoralis* Boisduval was introduced to Mauritius, probably with cash crops from Africa or Europe. The most abundant Lepidoptera species was the Microlepidoptera *Nacoleia* sp.1, which is not yet described in the literature despite the fact that the Lepidoptera are the best-described order of Mauritian invertebrates. The endemic butterfly *Dysauxes florida* Joan.

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accounted for 36.2% of all lepidopteran flower visits in the unrestored site, but in the restored site it was less than 0.1%.

Only two species of Coleoptera were introduced to Mauritius, although the majority of species could not be identified and thus, their origin could not be determined (Fig. 15). Nevertheless, one introduced species, *Chaetocnema* sp., was not only overall the most generalised and one of the most abundant flower visitors in the unrestored site (see Fig. 2), but is also accounted for 93.2% of Coleoptera visits in the unrestored site. *Chaetocnema* sp. mainly visited flowers of *S. lineata* in both sites, in addition to *P. cattleianum* in the unrestored site (see Appendix VIII; H, M, R).

Ant flower visitors were approximately four times as abundant in the restored as in the unrestored site, although the ratio of native and introduced ant species was similar in both sites (Fig. 16). The plant–ant visitation web had the highest connectance of all webs (see Table 4). Native *Brachymyrmex* sp. and introduced *T. albipes* were rarely observed to share floral resources of the same species, with the exception of *A. theiformis,* which was heavily used by both ant species. *Brachymyrmex* sp. was the most common flower visitor of *P. terebinthina*, a plant species, which was rarely visited by *T. albipes.* On 55.6% of plant species visited by *T. albipes*, foraging ants were observed only once or twice, suggesting a low fidelity to many floral resources.

Of the four observed vertebrate flower visitors, the two generalist bird species, the Madagascar Fody *Foudia madagascariense* and the Red-whiskered Bulbul *Pycnonotus jocosus* were both introduced to Mauritius, and these were observed only once to forage for nectar on flowers in the restored site. In contrast, the endemic Grey White-eye *Zosterops mauritianus* and the Blue-tailed Day Gecko *Phelsuma cepediana* were regular flower visitors of 16 plant species in the restored and four in the unrestored site. Of the plant species which occurred in both sites and were visited by endemic vertebrates in the restored site, 11 species were not visited by vertebrates in the unrestored site. Ten out of 11 plant species visited by *Phelsuma cepediana* were also visited by *A. mellifera*, suggesting resource competition between introduced and endemic pollinators.

DISCUSSION

Strength and limitations of the study

Our study presents two of the most extensive and comprehensive fully-quantified plant–pollinator visitation webs to date. The visitation webs include all woody flowering plant species which flowered between August 2003 and April 2004 independent of their flowering time (diurnal or nocturnal), of the length of their flowering period and of their range of pollinator species. The identification of flower visitors to species level resulted in highly resolved webs, and the methodological setup of repeated fortnightly sampling led to a high temporal and spatial resolution of the webs. We included several temporal and spatial dimensions to minimise the chance of sampling bias (see Waser *et al.* 1996). Nevertheless, there are a few inherent problems to surveying entire plant–pollinator communities. The depiction of the overall webs neglects that not all pollinators and flowering plants occurred simultaneously and within a small, spatially confined area, so that not every pollinator species had unrestricted access to each plant species. However, the majority of potential links were impossible due to phenological or spatial uncoupling of plants and pollinators. Overlooking such "forbidden links" (sensu Jordano *et al.* 2006) may result in underestimating network connectance, and consequently underestimating the degree of generalisation of the communities.

Another shortfall of focusing on the community level is the loss of accuracy with respect to pollination efficiency of individual flower visitors. Flower visitor is not necessarily synonymous to pollinator, though the terms have been used interchangeably in this study, because even if flower visitors transport pollen they can vary in pollination efficiency (e.g. Schemske & Horvitz 1984). Thus, visitation web studies do not replace experimental studies regarding, for instance, interaction strength between two mutualistic partners in relation to other species in the community. However, visitation webs complement such studies in making educated extrapolations from experimentally demonstrated mechanisms to effects in a real community (Cohen *et al.* 1993).

Due to the scarcity of heath habitats in Mauritius and the intensity of the data collection, the study could not be replicated over several restored and unrestored sites. Therefore, it is statistically problematic to assign the differences between the restored and unrestored sites to the habitat restoration scheme applied in the CMA. However, the findings presented in this study indicate that the structural differences in the plant and pollinator communities are tied to alterations caused by habitat restoration in the CMA. We statistically controlled for spatial and phylogenetic dependencies between plant and animal species to

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minimise the effects of pseudo-replication and to elucidate honest biological differences between communities of both sites.

The heterogenic structure of the plant community with many rare and few abundant species made it difficult to collect representative information on fruit set during fortnightly fruit counts for all plant species at each site. Fruit set of rare plant species and species with rapidly developing fruits or a high rate of fruit predation have been underestimated with our methods. Finally, we may underestimate the importance of birds in the pollinator community because of fewer observations were carried out before 7 am, the time when birds were most active in the study area (Hansen *et al.* 2002).

Objectives of this study

The three objectives of this study were to investigate plant–pollinator community structure, to identify key species and to estimate the effects of introduced species on the community structure. Results indicated that the community structure was more complex in the restored than the unrestored site. The former showed higher plant linkage, pollinator diversity and abundance, but visitation rates for plant species that occur at both sites were similar. Plant species in the restored site produced larger and heavier fruits and their fruits contained more seeds per fruit than those in the unrestored site. Vertebrate pollinators were rare in the unrestored site, but relatively abundant and highly linked in the restored site. The pollination systems in both sites were highly generalised with a few super-abundant, well-linked pollinator species utilising the majority of flowering plant species in the communities. However, most of the animal key species were introduced to Mauritius. In contrast, introduced plant species, although some of them being the most abundant species in the unrestored site, interacted directly only with few pollinator species. In the following sections we will discuss these results in more detail and highlight implications for restoration management.

Community structure

Visitation webs

Both the restored and the unrestored site were similar in terms of native plant species composition. However, the habitat structure in the unrestored site was heavily altered by the presence of alien invasive plant species. The natural, semi-open heath structure gave way to dense growth of the introduced shrubs *Psidium cattleianum* and *Wikstroemia indica*, interspersed with native plant species (see Appendix II). Several species which were formerly

wide spread in the upland areas of Mauritius (Vaughan & Wiehe 1937), are now extremely rare, occurring only locally in tiny numbers in Pétrin CMA and the unrestored site, e.g. *Claoxylon linostachys* ssp *brachyphyllum*, *Polyscias neraudiana* (did not flower during the study period), *Chassalia petrinensis*, *Xylopia lamarckii* and *Badula platiphylla*. With the exception of *C. linostachys,* we did not observe developing fruits on any plant individual of those species for more than two consecutive flowering periods, and records on fruiting events from recent years were very sporadic, despite regular surveys (JC Sevathian, M Allett pers. comm.).

Most flower visitors in both sites were extremely rare (~48% with one or two interactions), which is similar to numbers presented by Petanidou and Potts (2006) on species-rich Mediterranean pollinator communities. Dipterans were the most abundant flower visitors, a pattern commonly observed in pollination assemblages in high latitudes (Elberling & Olesen 1999 and references therein), high altitudes (Arroyo *et al.* 1982, Primack 1983, Inouye & Pyke 1988, Kearns 1992, Dupont *et al.* 2003, but see Ollerton *et al.* 2006) and on islands (Anderson *et al.* 2001, Rathcke 2001). Although attention is often focused on bees and vertebrate pollinators, many Diptera taxa are anthophilous, i.e. are associated with flowers in most parts of the life cycle (reviewed in Larson *et al.* 2001), and they have been widely acknowledged as potential pollinators of many plant species (Motten 1986, Kearns 2001). From the plant's perspective, generalist flies compensate their inefficiency as pollinators (Faegri & van der Pijl 1979) with their abundance, particularly when more efficient pollinators are absent (McGuire & Armbruster 1991, Kearns & Inouye 1994). The differences in Diptera diversity and abundance between sites could be due to local variation in fly numbers (Herrera 1988). Dipteran visitation rates may be particularly affected by abiotic factors, floral density, plant composition and competition for resources with other flower visitors (McCall & Primack 1992, Kearns & Inouye 1994), and fluctuations are likely to occur between years (Herrera 1988, Pellmyr & Thompson 1996). The latter, however, is certainly true for most invertebrate and vertebrate pollinators (Petanidou & Ellis 1993, Fishbein & Venable 1996, Price *et al.* 2005).

Pollinator species richness and density are important measures in defining the integrity of a habitat and its ecosystem functions (Kevan 1999, Larsen *et al.* 2005). Rarefaction curves indicated that the pollinator assemblage in the restored site was significantly more species-rich than that of the unrestored site. However, the species richness estimator suggested that the two sites did not differ in their species diversity. Species density, as in the number of species per unit area, could also be compared by rarefaction curves when the sampling was

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standardised on the basis of area or sampling effort (Gotelli & Colwell 2001). Thus, we can infer that pollinator species density was higher in the restored than in the unrestored site. Despite the extensive sampling effort, both the rarefied species accumulation curves and the species richness estimators did not reach an asymptote, which is a common pattern in assemblages with many taxa (e.g. tropical habitats, microbial communities). However, it still allows a comparison of the curves themselves (Novotny & Basset 2000). In this case, the estimators should be viewed as providing only a lower-bound estimate of species richness (Gotelli & Colwell 2001).

All flower visiting vertebrate species were more abundant and more highly connected in the restored compared to the unrestored site. The role of geckos in pollination has been considered vital to the reproduction of many native Mauritian plants species (Olesen *et al.* 1998, Nyhagen *et al.* 2001, Hansen *et al.* 2006), and on other islands (Olesen & Valido 2003). The endemic gecko *P. cepediana* is an important pollinator of several endangered plant species in Pétrin, e.g. *Trochetia blackburniana* (Hansen 2006) and *Roussea simplex* (Hansen 2005). Male *Phelsuma* geckos are territorial and their abundance is related to habitat structure and quality (Harmon 2005), especially to the occurrence of screw pines *Pandanus* spp. (Lehtinen 2002). The low structural diversity and the lack of suitable habitat for geckos in the unrestored site probably contributed to the low density of *P. cepediana* in the degraded habitat (Cole 2005). Similarly, the foraging behaviour of the endemic grey white-eye *Zosterops mauritianus* appear to be linked to habitat structure and the availability of floral resources (Hansen *et al.* 2002; see Chapter 2). Little is known about the pollination services provided by the two introduced, generalist flower visitors, the Madagascar fody *Foudia madagascariense* and the red-whiskered bulbul *Pycnonotus jocosus*. The former is closely related to the nectar-feeding endemic Mauritius fody *Foudia rubra*, which has been frequently observed visiting flowers of native and introduced plant species (Cheke 1987b), also in Pétrin (Safford 1991).

The five native plant species with the highest floral abundance *Aphloia theiformis, Stillingia lineata, Psidia terebinthina, Sideroxylon puberulum* and *Croton fothergillifolius* were visited by a total of 88 (65%) and 58 (58%) pollinator species in the restored and the unrestored site, respectively. Most of these visitors presumably sought pollen as reward since the majority of abundant plant species offered no or minimal nectar. Highly nectar rewarding plant species such as *Trochetia blackburniana, Roussea simplex, Turraea rigida, Syzygium venosum* and *Labourdonnaisia callophylloides* were only visited by a total of 14 pollinator species in the restored site, including all vertebrate species. Eight of these species visited *R. simplex*. This observation of few visitor species to highly rewarding plant species appears to

contradict the optimal foraging theory (Fretwell & Lucas 1969, Possingham 1992). One possible explanation is that nectar feeding insects in the study area were formerly more diverse and abundant before becoming locally extinct (Mauremootoo *et al.* in press-b). A second possibility is that the hexose-dominated nectar of nectar-rich species in Pétrin (*Syzygium* spp., CN Kaiser, unpublished data; *R. simplex, T. blackburniana* and *T. rigida*, DM Hansen, pers. comm.) may be an adaptation to vertebrate pollination (Baker & Baker 1983) and, thus, the floral displays of such plants attract fewer invertebrate flower visitors.

Plant communities

Empirical studies suggest that plant population density may be positively correlated with pollination success and seed set (e.g. Silander & Primack 1978, Klinkhamer *et al.* 1989). In our study, plant abundance was an indicator for local plant population density, and abundance of most native plant species was higher in the restored than in the unrestored site. We also showed that plant abundance was positively related to the number of pollinator species and the visitation rate of a plant species. The relative plant frequency of rare or locally rare species was lower in the unrestored than in the restored site due to the high density of *P. cattleianum.* This could have detrimental effects on the quality and quantity of pollen dispersal of native plants species in the degraded area (Oostermeijer *et al.* 2000). Small-scale changes in plant density and relative frequency may alter the foraging behaviour of pollinators, and habitat structure is an important criterion for territorial vertebrate pollinator when choosing a territory (see section on vertebrate pollinators). Although even small insects are capable of long-distance pollen dispersal (e.g. Harrison 2003), it has been shown that spatial isolation on the level of neighbouring plant species has resulted in reproductive decline for a variety of plants (Burd 1994, Knight *et al.* 2005). For example, if plant density is low, pollinators may visit more flowers on the same plant thereby increasing level of inbreeding (Karron *et al.* 1995, Kunin 1997). Ghazoul (2005) reviewed the effect of relative abundance (also called purity) of plant species on pollination and reproductive success; six out of 11 studies showed a decline in pollination due to decreased purity, and eight out of nine studies indicated reduced reproductive success as a consequence of decreased purity. Flower colour is a cue for pollinators when foraging for floral resources and many pollinators respond to the relative abundance of plants and/or flowers in a density-dependent manner (Smithson & Macnair 1997). The majority of plant species in Pétrin produce pale, inconspicuous and small flowers (see Appendix IX), and only a third of plant species offered detectable amounts of nectar. Given the lack of conspicuousness and nectar-rich flowers in the Pétrin plant communities,

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the invasion of introduced plant species, even if the actual abundance of native plant species remains unaffected in the short-term, is likely to have a considerable effect on the foraging behaviour of pollinators, and eventually on the reproduction of self-incompatible plant species.

A shorter flowering season or a shift towards flowering later in the season may have negative effects on reproductive success of native plant species. Cyclonic weather often terminates flowering abruptly, and the probability of such weather increases towards the end of the main flowering season. During our study, we were unable to show any effect of phenology on reproductive success, possibly because such effects can be highly species and population specific (see Ollerton & Lack, 1998, Ollerton & Diaz 1999). However, it is possible that, if plants in the population flower asynchronously, the effective population size will be reduced which could contribute to the likelihood of pollinator loss and affect plant reproduction in the long-term (Ghazoul 2005). Shifts in flowering time can also interrupt the seasonal timing of flowering and pollinator activity (Price & Waser 1998).

Plant reproductive success

Fruit size, weight and the number of seeds per fruit were higher in the restored than the unrestored site. Differences in fruit size and weight are unlikely to result from a shortage of nutrients in the unrestored site since soil nutrient content was similar between sites. Another explanation is the strong competition for water. Despite a high annual rainfall in the Pétrin area, droughts in the uplands of Mauritius occur frequently between November and December. During a six week period without rainfall (17 November – 26 December 2003), we observed multiple symptoms of drought stress (wilted leaves, aborted flowers) in the unrestored site, where plant density was much higher than in the restored site. Smaller fruit size and weight in the unrestored area may be associated with the scarcity of water (Schimpf 1977). Larger fruits have been shown to have a competitive advantage over smaller fruits since they provide increased nutrition to the seedling and possibly increased dispersibility by frugivores (Baker 1972, Wulff 1986). A higher number of seeds per fruit is a direct consequence of increased pollination success, which is a product of visitation rate and per-capita effectiveness or efficiency of pollinators (Waser & Price 1983, Herrera 1987, 1989). This, together with a fruit set that was marginally higher in the restored site suggested that pollination success was increased in the restored site, at least for some common plant species.

Structure of visitation webs

In terms of floral abundance, there were almost twice as many flowers in the restored site than in the unrestored site, and regarding quantified visitation rate, the web of the restored site was 1.8 times larger. The webs were characterised by a few abundant species and many rare species with weak interactions. Web connectance at both sites was relatively low (within the lower third) compared to 36 plant–pollinator systems compiled by Jordano (1987). However, compared to the analysis of another 29 webs presented in a more recent study (Olesen & Jordano 2002), our study systems belonged to the higher 25% of connected webs. We sampled entire webs unlike other webs which effectively subsampled the whole web. This could explain such discrepancy in connectance between our and other studies, since the higher connectance of many webs presented by Jordano (1987), were largely derived from webs based on only a subset of the pollinator fauna. We also corrected connectance for the extended sampling period (Medan *et al.* 2006), so a direct comparison with the values given by Olesen & Jordano (2002) is not suitable. When seasonality in connectance is not taken into account (see Fig. 4), more than 50% of Olesen & Jordano's webs (2002) had a higher connectance than the pollination systems in Pétrin.

Connectance is dependent on network size (Jordano 1987), which may be linked to sampling effort (Ollerton & Cranmer 2002, Herrera 2005), and differences between tropical and temperate pollination system's connectance may be attributable to such variation in species richness. Therefore, the use of connectance as an index of generalisation is questionable (Kay & Schemske 2004, but see Petanidou & Potts 2006). A single macroscopic description such as connectance may not adequately characterise the organisation of complex networks (Melian & Bascompte 2004). Average generalisation level in pollination systems may be a more suitable measure of network structure since, unlike connectance, it is independent on network size and is less likely to be underestimated when subsets of networks are sampled (Waser *et al.* 1996).

Key species and generalisation

Key animal species

The most abundant and highly linked flower visitors were the introduced honey bee *Apis mellifera,* the fly *Stomorhina lunata,* the ant *Technomyrmex albipes* and the beetle *Chaetocnema* sp, and the native ant *Brachymyrmex* sp. The dominance of a few pollinator species suggests a low level of interspecific competition in the pollinator communities, which was also described for other island communities (Diamond 1975, Whittaker 1998). One

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reason for the high visitation frequency of most of these super-abundant flower visitors may be their prolonged flight season (or for flightless pollinators: foraging season). Honey bees commonly forage throughout the entire season (Goulson 2003), which can have contrasting effects on the associated native plant–pollinator community: the long foraging season results in an overlap in foraging time with most co-occurring pollinator species and the honey bee is therefore a strong competitor for floral resources (e.g. Dupont *et al.* 2004). At the same time, honey bees may be beneficial, by ensuring pollination to many wildflowers and crops (see also section "Introduced species"). Honey bees, being social insects, usually occur in large numbers. Due to their abundance and generalist foraging pattern, they can serve as pollinators to rare plant species, where the original pollinators may be extinct. In contrast to findings from Mediterranean plant–pollinator communities, honey bees were equally associated with common, generalist plant species and poorly visited, rare plant species (Petanidou & Potts 2006). However, our findings on asymmetrical specialisation indicated that highly generalised introduced pollinators tended to visit more specialised plant species, and thereby potentially filled gaps caused by the absence of the original pollinators (see Fig. 11).

Not all flower-visiting animals are pollinators and the pollination efficiency of those that are pollinators varies with plant species (Stebbins 1970, Schemske & Horvitz 1984). Total pollination success is a product of visitation rate (pollination quantity) and per-visit efficiency (pollination quality) (Waser & Price 1983, Herrera 1987, 1989, Campbell *et al.* 1996). Most pollination community studies neglect this species-specific variation in pollination efficiency and therefore the subsequent contribution to pollination of each plant species can vary greatly (Olesen *et al.* 2002, Potts *et al.* 2003). However, Vazquez *et al.* (2005) advocated that the visitation frequency of a flower visitor (i.e. pollination quantity) is an appropriate surrogate for per-capita pollination efficiency, i.e. the importance of a pollinator species to the pollination success of a given plant species can be largely assessed by pollinator visitation, and pollinator efficiency plays a smaller role (see also Motten *et al.* 1981, Olsen 1997). In this study, we only recorded flower visitors that made contact with the sexual parts of the flowers, thus our measure of visitation rate, despite ignoring detailed biological parts of the interaction, should closely approximate the importance of flower visitors to given plant species. Nevertheless, for some groups of flower visitors the contribution to the pollination between conspecifics within or between populations is dubious. Ants, for example, are unlikely to cross-pollinate despite their abundance as flower visitors because wing-less workers have to crawl to reach flowers, and pollen transport between different plants is therefore unlikely (Beattie *et al.* 1984, Proctor *et al.* 1996). If pollination

occurs, the plant species are either specialised for ant-pollination (Peakall *et al.* 1991, Sugiura *et al.* 2006) or subject to a high relative abundance of ants as flower visitors in comparison to other winged-pollinator taxa (Gómez *et al.* 1996). In summary, most pollinators which interact frequently with many plant species in the community probably contribute considerably to the plant's pollination success even if they are not the most effective pollinators.

Generalisation of plants and pollinators

Plant species in the restored site interacted with an average of 10.1 pollinator species, almost two species more than in the unrestored site. Animal species at both sites, however, showed a similar degree of generalisation (see Table 1). While the generalisation level of plant species in our study lies well within the range of linkage values from the 29 plant–pollinator communities presented by Jordano *et al.* (2006), the mean linkage of pollinator species is at the upper end of the scale of generalisation for the webs reported by the authors (one community with more generalist pollinators). This is somewhat surprising given that, in both of our study sites, approximately 50% of pollinator species interacted with only one plant species. However, both communities may best be characterised by several highly generalised flower visitors, which were also relatively abundant in both communities. The plant linkage observed in the Pétrin communities is indeed within the range of communities reported by Jordano *et al.* (2006), but comparatively high when we consider that linkage of island plants tends to be lower than that of mainland plant species (Olesen & Jordano 2002). We can summarise that the plant and pollinator communities in Pétrin were relatively generalised in their mutualistic interactions, which is a common feature of many island plant–pollinator communities (Primack 1983, Barrett 1996, Bernardello *et al.* 2001, Anderson 2003).

Competition and facilitation between plant species for pollination have long been focal points of research for pollination biologists (e.g. Rathcke 1983, Campbell & Motten 1985, Moeller 2004), but little is known about the effects of such processes on community structure. Plant species which interact with many pollinator species, and *vice versa*, may be important for the structure and stability of plant–pollinator communities. Generalist plant and pollinator species have a high resource overlap, which may result in strong direct and indirect competition for floral resources (between pollinator species) or for pollination services (between plant species). In our study, the most dominant and generalised pollinators (key species) were introduced invertebrates. To invade new habitats, those species utilise floral resources offered by resident plant species, which may increase the competition with native

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pollinators. Honey bees show substantial niche overlaps with native pollinators such as birds and bees (Goulson 2003 and references therein), and consequently native pollinators are often displaced to less profitable sources of food (Ginsberg 1983, Hingston & McQuillan 1999). The stability of plant–pollinator communities is thought to increase with a high degree of redundancy in pollinators because adverse events are unlikely to affect all species equally severely (Lawton 1994, Kearns 2001). For instance, Memmott *et al.* (2004) showed that the tolerance of plant–pollinator communities to species extinctions derived from redundancy of pollinators. In our unrestored site, almost 20% of plant species received less than three visitors compared to 10% in the restored site, and overall, plant species were more generalised in the restored than in the unrestored site. If a high level of generalisation can "secure" against the collapse of plant–pollinator webs and therefore be used as a descriptor for the functional integrity of a system, the unrestored site is of lower integrity than the restored site. On a pollinator level, generalist flower visitors such as honey bees or syrphid flies may have dampened the effects of local absences of native pollinators on plant species with open, easily accessible flowers, which attract a broad range of floral visitors (see also section "Introduced species in visitation webs").

The positive relationship between generalisation and the mean visitation rate of plant species found in this study is similar to findings of other studies which have described the relationship between generalisation and visitation frequency of pollinators (Vazquez & Aizen 2003). This association may be a true biological mechanism or due to a sampling bias because rare species are likely to be observed less often than abundant species. Even in comprehensive community surveys, such sampling biases are almost unavoidable, and may affect network properties. In food web studies, sampling bias has been proposed as an explanation to describe certain food web properties (Goldwasser & Roughgarden 1997, Bersier *et al.* 1999). There are several biological mechanisms which may account for the relationship between generalisation and visitation rate. Firstly, abundant plant species are more likely to be encountered by pollinators than rare plants and therefore receive more visitor species (see section asymmetrical specialisation). Secondly, abundant plant species simply flower for an extended length of time and, thus, interact with more pollinator species (Vazquez & Aizen 2003). Since plant relative abundance and length of flowering were reduced in the unrestored site, these mechanisms may have acted either individually or in combination.

Asymmetrical specialisation

The negative, albeit weak, relationship between the degree of specialisation of plant species (s_i) and the mean specialisation of their pollinator species (p_i) indicates a tendency towards

asymmetrical specialisation, i.e. generalist plant species attract more specialised pollinator species, whereas specialist plant species were more likely to interact with generalist pollinators. Although s_i and p_i of animal species was not correlated, this relationship was also true for animal species; specialists did not necessarily visit specialist plant species and the same applied to generalists. Similar levels of asymmetrical specialisation in plant–pollinator webs have been shown from montane forest-communities in Argentina (Vazquez & Simberloff 2002) and from highly diverse Mediterranean communities (Petanidou & Ellis 1996, Petanidou & Potts 2006). We showed that our plant-pollinator communities are highly nested (sensu Bascompte *et al.* 2003; see also Chapter 7); that is specialist species mostly interact with a subset of the interaction partners of the more generalised species. Such asymmetries in specialisation may help to explain patterns of dependencies in mutualistic webs, diversity and long-term coexistence (Bascompte *et al.* 2006).

Introduced species in visitation webs

Structure of taxonomical subsets of visitation webs

Connectance of visitation webs of taxonomical subsets and mean linkage were not significantly different between sites and native and introduced pollinators. Only native pollinator species appeared to interact with more flowering plant species in the restored than in the unrestored site. However, the ecological significance of parts of these findings is questionable since most animal groups were represented by only one or two native or introduced species. In the Diptera, for example, where the comparison between mean linkage of native and introduced species were possible, both groups showed similar and relatively low linkage (see Table 4).

Some animal orders/families in our study were dominated by introduced species (e.g. Hymenoptera, Coleoptera), in others the ratio between introduced and native species was relatively balanced (e.g. Diptera, Formicidae), and introduced pollinators were almost absent from the Lepidoptera. Consequently, introduced species from some orders appear to encounter varying biotic or abiotic resistance, which influences the likelihood to establish natural populations. Some Diptera species are associated with livestock and have probably been repetitively introduced to Mauritius, which increases the chance of successful infiltration of the pollinator communities, e.g. in Pétrin. Honey bees were introduced to Mauritius for apiculture and feral colonies inevitably became established. The patterns of lepidopteran species richness and abundance, however, were intriguing. Lepidoptera were almost twice as species rich in the restored as in the unrestored site and mainly native and endemic

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Lepidoptera species were observed during the study. Despite being recognised as an important group of pest species in Mauritius (Mamet & Williams 1993), introduced Lepidoptera appear to be associated mainly with crop species and few species may have adapted to the harsh climatic conditions in the upland of Mauritius. Butterflies and moths are flower visitors feeding mainly on nectar (Proctor *et al.* 1996), which may be one explanation why few introduced lepidopteran species have entered the communities. The higher relative abundance of nectar producing plant species in the restored site may explain the higher species diversity in this site. An exception was the high abundance of the endemic butterfly *Dysauxes florida* in the unrestored site. The occurrence of this species was perhaps related to the plant species *Myonima violaceae*, which is used as a mating ground for the butterfly species. Neighbouring plant species with similar umbelliform flower heads such as *Psiadia terebinthina* and *Faujasiopsis flexuosa* were also frequently visited by *D. florida.*

Native versus *introduced*

Island ecosystems are particularly prone to species invasion (Simberloff 2000), partly because island biotas present less biological resistance to invaders (e.g. Elton 1958, Simberloff 1986). The eight introduced plant species at the unrestored site accounted for almost 83% of all plant individuals in the area. Two of the invasive species *Psidium cattleianum* (Strawberry Guava) and *Clidemia hirta* D. Don (Melastomataceae) are listed amongst the 100 world's worst invasive alien species by the Global Invasive Species Database (http://www.issg.org/database/species). Despite their dominance in the plant community, the invasive alien species appeared to compete only minimally for pollination with native plant species. Introduced plant species showed low linkage: three species (*Ossaea marginata, Clidemia hirta, Ardisia crenate*) received no visitors and only one visit was observed to *Wikstroemia indica*. This implies that these introduced species rely little on the local pollinator community for reproduction. Similarly, Memmott & Waser (2002) described fewer flower visitors on alien species in plant community in central USA. Given the abundance of fruits produced by all introduced plant species in this study, the shortage of flower visitors appeared to have little effect on their reproductive performance. The high fruit set of introduced plant species may be ascribed to the occurrence of autogamy, a common strategy to overcome pollen limitation by invasive alien plant species (Baker's rule; Baker 1967, Rambuda & Johnson 2004). It has also been suggested that plant invaders have a higher chance of success if they have a generalised pollination system (Baker 1986). Indeed, those introduced plant species in our study system which were visited by pollinators attracted a

wide range of visitor species, e.g. *Homalanthus populifolius* (l = 18) and *P. cattleianum* (l = 11).

Introduced insects, in contrast to introduced plant species, have attracted less attention in Mauritius, largely due to the conspicuous devastating effect of plant invaders on the native habitat. Introduced insects have previously gained attention primarily as sugar cane pests or as bio-control agents which were deliberately introduced to control for such pests (Williams & Ganeshan 1999), but no reliable information exists on the effect of introduced insects on the native biodiversity of Mauritius (Mauremootoo *et al.* in press-b). Despite good knowledge on the effects of vertebrate and plant invaders on many island ecosystems, there is a lack of research on island invertebrate communities, also reflected by the high number of insects which could not be determined to species level (ca. 53%). Until recently, research on introduced invertebrates concentrated on areas where human activities were directly affected by, e.g. pest species in agricultural systems or beneficial mutualists as providers of ecosystem services to crops (see Chapter 5). Hence, few studies have investigated the effects of introduced insects on the native invertebrate diversity.

The pollinator community of Pétrin (both sites) was composed of 35 introduced and 45 native/endemic animal species (the origin of another 814 species could not be identified). Native and endemic pollinators accounted for only 28% of visits whereas introduced animals accounted for 63% (unknown origin 9%), which illustrates the dominance of introduced pollinators in the communities. Although these numbers may not reflect the contribution of native or introduced flower visitors to pollination, they provide a possible explanation for the demise of native pollinator diversity in Pétrin. Both sites had similar numbers of introduced pollinator species, and the elevated visitation frequency in the restored site was probably related to the higher plant species richness and floral abundance.

The dominance of introduced flower visitors may affect the native pollinator community in many ways, but two effects are of main concern. Firstly, introduced species may be stronger competitors than native flower visitors for nectar and pollen (e.g. Butz Huryn 1997), which may result in the displacement of native species. Secondly, introduced species may be less efficient pollinators than native animals, especially for rare or more specialised plant species. The order of Hymenoptera was almost exclusively represented by introduced species; honey bees can compete with native pollinators for resources (Butz Huryn 1997) and were shown to pollinate native plant species, e.g. in Australia, less efficiently than native pollinators (Paton 1993, Paini 2004). In our study, almost all abundant plant resources were heavily exploited by introduced, often extremely abundant flower visitors, which can result in

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negative effects on plant reproduction and native pollinators (Hansen *et al.* 2002). The abundance of honey bees has also been shown to negatively affect the foraging behaviour of native bees (Eickwort & Ginsberg 1980). Despite the lack of studies of competition between native and introduced dipteran flower visitors, similar effects cannot be excluded.

Introduced plant and animal species can also facilitate each other's invasion (Simberloff & von Holle 1999, Richardson *et al.* 2000). Such synergistic interactions may explain the high abundance of the introduced beetle *Chaetocnema* sp in the unrestored site. Beetles mainly rely on pollen as a source of energy and *Chaetocnema* sp were predominately found on abundant, pollen offering species. Flowers of *P. cattleianum* in the unrestored site offered vast amounts of pollen, and thus *P. cattleianum* was one of the main foraging species of *Chaetocnema* sp. Since *P. cattleianum* is ubiquitous in the National Park, it provides a reliable stepping stone for associated animals to colonise new habitats. Whether *P. cattleianum* benefited from the presence of the beetle in terms of increased pollination is unknown.

In summary, introduced plant species were a main structural component distinguishing restored from unrestored habitat. Introduced plant species appeared to compete with native plant species for soil nutrients and water but less so for pollination because most introduced plant species did not depend on pollinators for reproduction. Introduced pollinators were the most abundant and generalised flower visitors providing the base for a high degree of competition for floral resources with native pollinators. The ratio of introduced to native pollinator species may appear to be biased towards introduced pollinators, because most insects of unknown origin are likely to be native (or very recent introductions which have not yet been described from Mauritius). However, most unidentified pollinators showed few interactions so even if they are all native, the impact of introduced pollinators would remain high.

Implications for conservation

The degradation of the heath habitat in some areas of Pétrin by invasive alien plant species had a significant effect on the structure and the diversity of plant and pollinator assemblages in these areas. The pollinator community in the unrestored site was less species-rich, less functionally diverse and less abundant compared to the community in the restored site. Similarly, native plant species in the unrestored site showed a decreased reproductive performance, lower plant species richness and strongly reduced relative abundance compared to the plant community in the restored site. At first, strong competition between introduced

and native plant species for nutrients and space may have inhibited native plant growth, and this process is ongoing in the degraded habitat. In addition, reduced plant reproduction may be a consequence of changes in the spatial distribution of plant species (Ghazoul 2005): when plant individuals become more isolated, pollination and seed dispersal begin to function less efficiently resulting in a decline in plant population density or relative abundance and in a disproportionately steeper decline in reproductive output. The signs of degradation observed in the unrestored area closely resembled these descriptions and, for some plant species at least, appeared to be approaching the final step where relative plant abundance is low and reproductive output is reduced compared to more natural conditions in the restored site. Indeed, we would not expect the same suite of effects to act on all plant species in the unrestored system as plants use a variety of reproductive mechanisms (or a range of pollinators) to react to altered conditions (Bond 1994). In particular, isolated or small plant populations cease to stay reproductively viable. To overcome the spatial effect of population decline, conservation projects should aim to restore areas large enough to maintain viable population sizes for rare species in the area whereby the structural diversity will be maintained. If sufficient large areas are not available, *ex situ* plant propagation of rare species should complement *in situ* restoration schemes and plantation or native and endemic plant species could supplement natural populations. To increase pollination success of planted species, we suggest accounting for spatial components, such as the foraging distance of pollinators, and planting individuals of the same species in groups.

The pollinator assemblages in both sites were dominated by introduced, generalist flower visitors indicating that, for common animal species, the structural difference between the plant communities had little effect on their foraging behaviour. However, pollinator species richness and density was higher in the restored site, which may be directly linked to habitat restoration. For example, bird and gecko flower visitation was almost absent in the unrestored site, and both groups of pollinators were shown to be sensitive to changes in plant community composition (Chapter 2, Hansen 2006). The reliance of geckos and birds on a certain habitat structure makes them valuable bio-indicators of habitat quality (see Kevan 1999). The relationship between habitat structure and pollinator assemblages described in this study has strong implications for the conservation of other degraded habitats in Mauritius, on other oceanic islands, but also in degraded mainland ecosystems.

The diversity of a plant community may be related to the functional diversity of its pollinator community (Fontaine *et al.* 2006), and species-rich floras support a higher diversity of pollinators (Kevan 1999). Differences in floral abundance affect foraging decisions of

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insects (Faegri & van der Pijl 1979, Waser & Real 1979, Feinsinger 1987, Armbruster *et al.* 2000), and insects concentrate their foraging on dense patches of flowers (Thomson 1981), which are more common in the restored site due to the higher relative abundance. To maintain pollinator species diversity one has to preserve structural diversity (Potts *et al.* 2003, Larsen *et al.* 2005) to provide food sources, nesting and oviposition sites, and resting or mating sites (Kevan 1999). In Mauritius, structural diversity should also be maintained during the restoration process, which may be achieved by low-impact follow-up restoration (here: weeding invasive alien plant species). Although the initial weeding is necessarily of high-impact to the plant and pollinator community, subsequent weeding events should be of minimal disturbance to ensure long term increase in structural and species diversity.

Conclusion

We showed that visitation web studies are useful tools for elucidating differences in plant–pollinator assemblages between two habitats, which are similar in plant species composition but fairly distinct in plant and pollinator community structure. Our findings suggest that habitat restoration is crucial for maintaining functional ecosystem integrity. Higher pollinator species richness and abundance in the restored site indicate a positive effect of habitat restoration on the pollinator diversity, which may increase community stability and secure a higher rate of pollination success of native plant species. This study also showed that the pollinator assemblages in Pétrin are infiltrated by introduced invertebrate species, which can accelerate the decline of native pollinators through competition and simultaneously begin to fill the role of missing pollinators. However, pollinator niches for native plants are likely to remain empty because introduced pollinator species are likely to be generalists and therefore, are less well adapted, evolutionarily and ecologically, to act as effective pollinator of more specialised native plant species. For habitat restoration to be successful in the long-term, practitioners should maintain structural diversity to support a species-rich and abundant pollinator assemblage which ensures native plant reproduction, despite frequent biotic and abiotic perturbations.

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TABLES

Table 1 Visitation web parametres of the restored and the unrestored site. We present the total number of plant (*P*) and animals species (*A*), visits (*V*), and interactions (*I*), as well as the ratio of animal per plant species, web size (*S*), connectance (*C*), mean plant (l_p) and animal linkage (l_a), and maximal plant and animal linkage (l_{max}).

Statistics	Restored	Unrestored
Number of plant species (*P*)	74	64
Number of animal species (*A*)	135	100
Number of visits (*V*)	3961	3334
Number of interactions (*I*)	744	534
Ratio *A/P*	1.84	1.56
Network size (*S*)	9990	6400
Connectance (*C*)	13.23	15.57
Maximal plant linkage (l_{max})	39	38
Maximal animal linkage (l_{max})	45	34
Plant linkage (l_p)	10.05 ± 1.06	8.34 ± 1.15
Animal linkage (l_a)	5.52 ± 0.71	5.39 ± 0.71

Table 2 Effect of site and species identity on fruit size, fruit weight and the number of seeds per fruit.

Trait	Source	*df*	MS	*F*	*p*
Fruit size	Site[1]	1	0.74	47.68	**< 0.0001**
	Species	13	3.42	238.31	**< 0.0001**
	Site × species	13	0.02	1.08	0.372
	Residuals	220	0.01		
Fruit weight	Site[2]	1	2.81	31.90	**< 0.0001**
	Species	11	26.00	246.80	**< 0.0001**
	Site × species	11	0.09	0.84	0.602
	Residuals	173	0.10		
Seeds/fruit	Site[3]	1	4.39	21.14	**0.002**
	Species	7	11.68	85.05	**< 0.0001**
	Site × species	7	0.21	1.51	0.169
	Residuals	133	0.14		

[1] Tested against the fruit size Site × species interaction

[2] Tested against the fruit weight Site × species interaction

[3] Tested against the seeds/fruit Site × species interaction

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Table 3 Effect of site, month and time of the day on mean temperature at ground level and humidity during pollinator observation sessions. Statistically significant results ($p < 0.05$) are indicated in bold.

Variable	Source	*df*	MS	*F*	*p*
Temperature	Site	1	20.3	1.69	0.194
	Month	3	220.8	18.35	**< 0.001**
	Time of day	1	8.3	0.69	0.408
	Site × month	3	70.4	5.85	**< 0.001**
	Site × time of day	1	143.6	11.93	**< 0.001**
	Month × time of day	3	25.5	2.12	0.098
	Site × month × time of day	3	207.7	17.26	**< 0.001**
	Residuals	439	12		
Humidity	Site	1	0.11	6.32	**0.012**
	Month	3	4.05	231.15	**< 0.001**
	Time of day	1	0.29	16.43	**< 0.001**
	Site × month	3	0.23	12.94	**< 0.001**
	Site × time of day	1	0.35	20.11	**< 0.001**
	Month × time of day	3	0.05	2.61	0.051
	Site × month × time of day	3	0.17	9.68	**< 0.001**
	Residuals	439	0.02		

Table 4 Visitation web statistics for subsets of taxonomic pollinator groups. Parametres are presented for the overall subset webs and for native and introduced pollinators separately. Column headings are as follows: number of animal species (*A*), the number of plant species (*P*) connectance (*C*) and mean ± SE linkage (*l*). Overall includes all pollinator species, i.e. native, introduced and those of unknown origin.

Site	Order	A_{native}	$A_{introduced}$	$P_{overall}$	$C_{overall}$	C_{native}	$C_{introduced}$	$l_{overall}$	l_{native}	$l_{introduced}$
restored	Aves	1	2	8	4.50	10.81	1.35	2.7	8.0	0.5 ± 0.0
	Coleoptera	1	2	23	4.05	4.05	13.51	1.8	3.0	9.0 ± 5.0
	Diptera	17	22	65	9.14	15.34	12.16	1.0	3.3 ± 2.4	2.6 ± 1.8
	Formicidae	1	2	49	29.73	27.03	31.08	16.3	20.0	22.5 ± 22.0
	Gecko	1	0	12	16.22	16.22	n/a	12.0	12.0	n/a
	Hemiptera	1	0	14	2.58	4.05	n/a	1.3	3.0	n/a
	Hymenoptera	1	4	46	7.99	1.35	19.59	4.2	1.0	11.0 ± 9.9
	Lepidoptera	17	1	38	4.73	4.45	1.35	1.3	1.6 ± 0.8	1.0
unrestored	Aves	1	0	2	3.13	2.70	n/a	2.0	2.0	n/a
	Coleoptera	1	2	36	5.56	8.11	26.35	2.0	6.0	17.0 ± 14.5
	Diptera	20	17	46	10.37	9.80	10.89	1.0	2.0 ± 1.6	2.2 ± 1.8
	Formicidae	1	2	27	19.27	16.22	16.89	9.0	12.0	12.0 ± 11.5
	Gecko	1	0	3	4.69	4.05	n/a	3.0	3.0	n/a
	Hemiptera	0	0	6	1.56	n/a	n/a	0.9	n/a	n/a
	Hymenoptera	0	3	32	8.33	n/a	18.92	3.6	n/a	9.7 ± 7.8
	Lepidoptera	9	1	32	7.44	6.31	1.35	1.9	2.9 ± 2.0	1.0

FIGURES

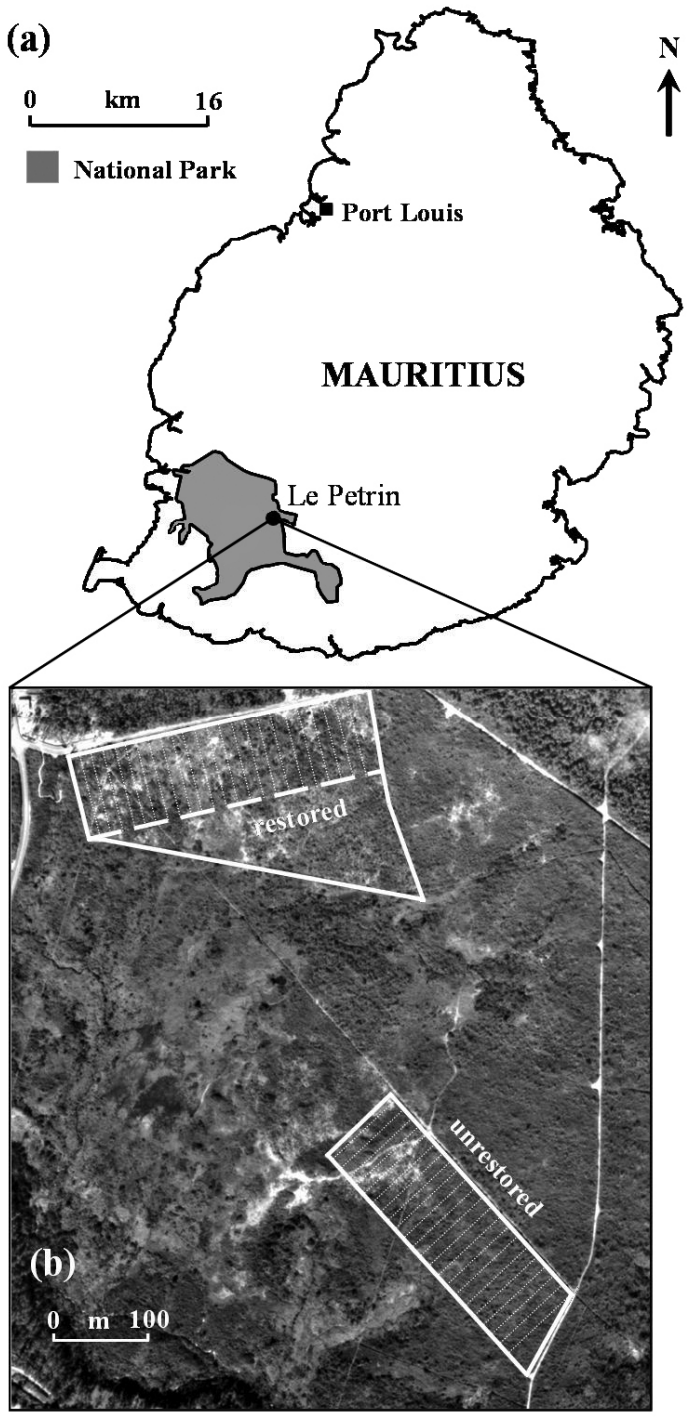

Figure 1 The island of Mauritius (a) with the Black River Gorges National Park and the study site Pétrin. The aerial photograph (b) shows Pétrin Conservation Management Area (CMA, restored) and the unrestored site in the study area. Within the CMA (represented by the solid line), the study was conduced in the rectangular part (separated by dashed line). Dotted lines indicate the arrangement of the sampling transects.

Figure 2 Quantified visitation webs for plant–pollinator communities in (a) the restored and (b) the unrestored site. Visitor species are shown as rectangles at the top and plant species are shown at the bottom (red rectangles depict introduced plant species). The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantified visitation rate between an interacting pair of species. Webs are drawn to the same scale. Full names to plant species abbreviations are presented in Appendix III. Animal species codes are only given for a selection of abundant pollinators referred to in the text. For all pollinator species codes see Figs. 12–16. Red: Hymenoptera, pink: Gekkonidae, light blue: Diptera, dark green: Aves, light green: Hemiptera, orange: Formicidae, dark blue: Coleoptera, and yellow: Lepidoptera.

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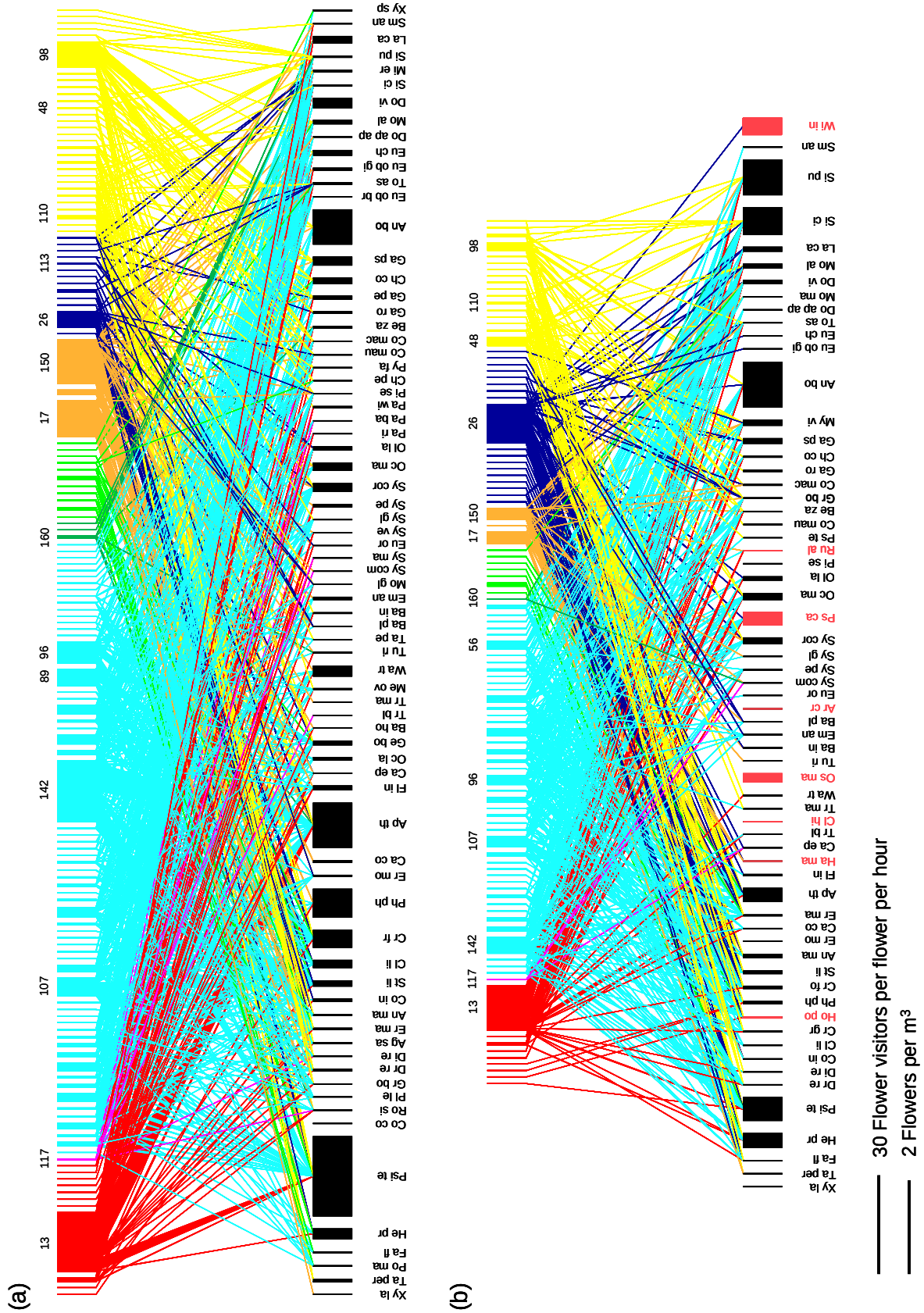
(a)
(b)
30 Flower visitors per flower per hour
2 Flowers per m³

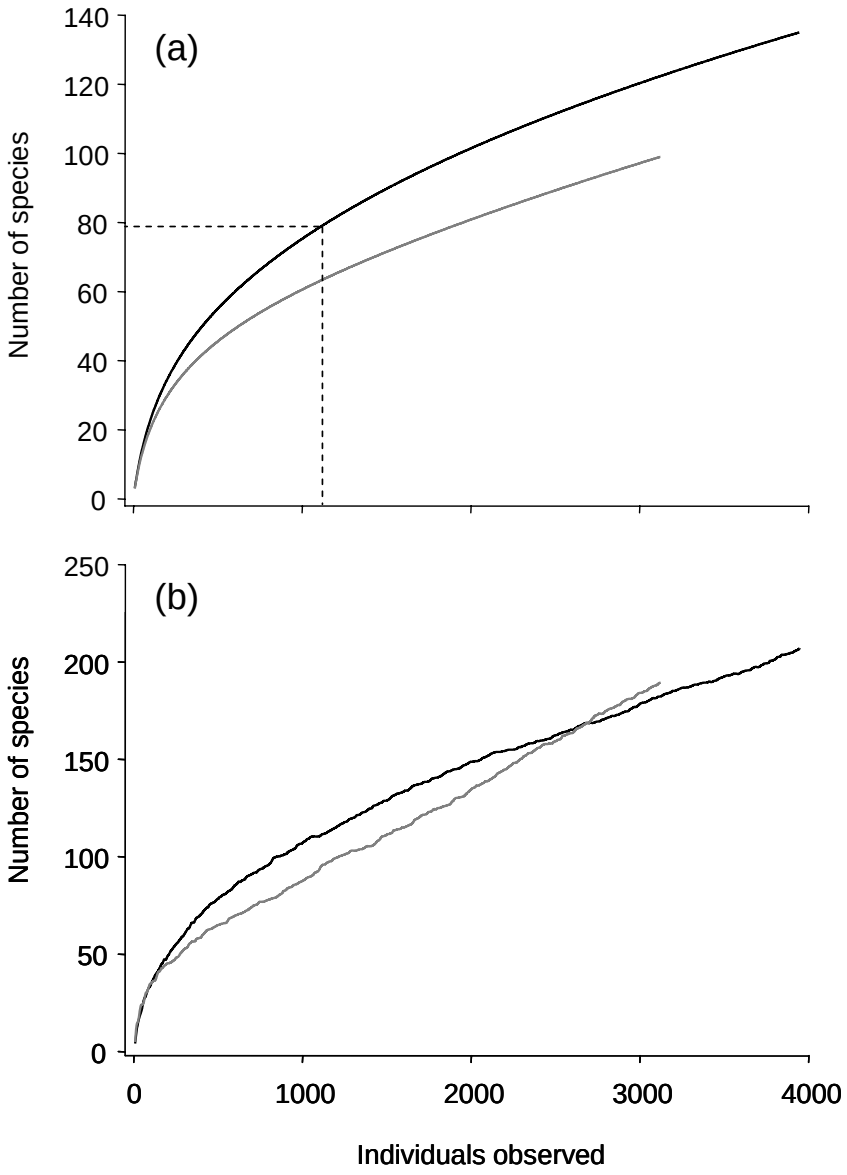

Figure 3 (a) Sample-based rarefaction curves and (b) abundance-based species richness estimators ACE, for the restored (black) and the unrestored site (grey). Rarefaction curves were compared by calculating 95% confidence intervals of the mean differences of both curves. The dotted line indicates the point where neither rarefaction curve overlapped with the confidence interval of the mean difference, i.e. when the two curves started to be significantly different ($p < 0.05$). The number of species is plotted as a function of the accumulated number of individuals since the individual carries the taxonomic information.

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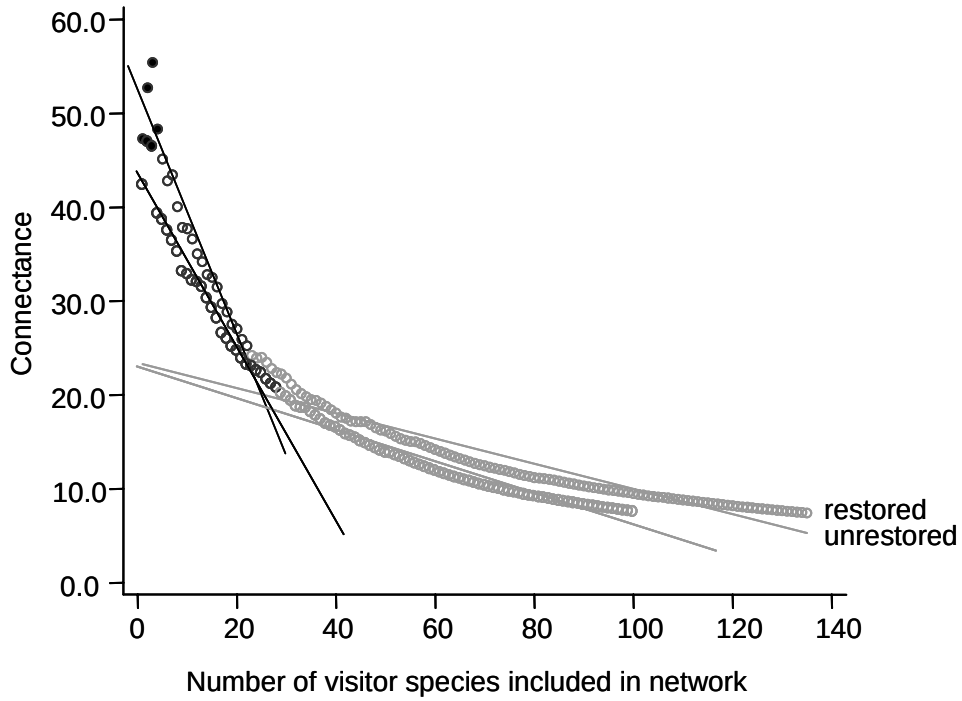

Figure 4 The effect of abundant (black circles) and rare (grey circles) flower visitors on network connectance in the restored and the unrestored site. Full circles depict the three most connected introduced pollinator species in the restored and the unrestored habitat (see Appendix IV for species names). Visitor species were sorted according to abundance, and connectance was calculated for each web after removing the given most connected animal species. The lines-of-best-fit show the contribution of the most abundant (black) and rare (grey) species to the overall connectance.

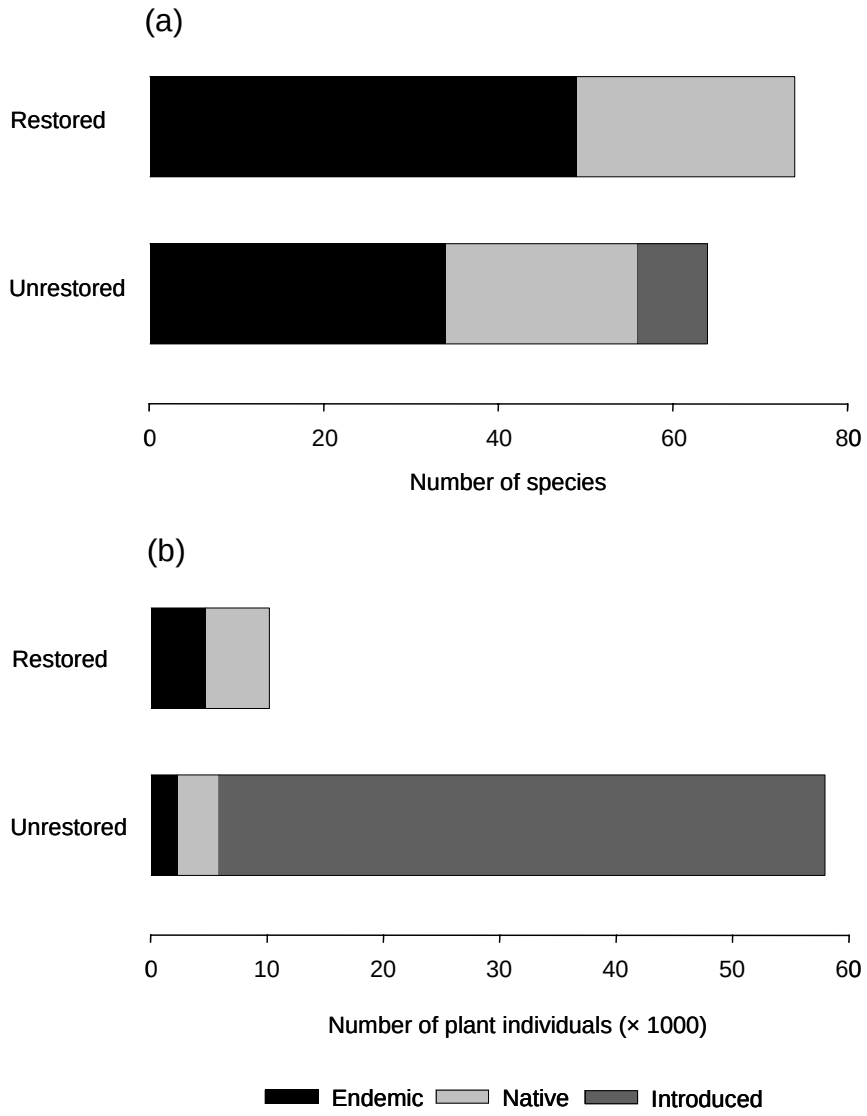

Figure 5 Endemic, native and introduced plant species (a) richness and (b) abundance in the restored and the unrestored site.

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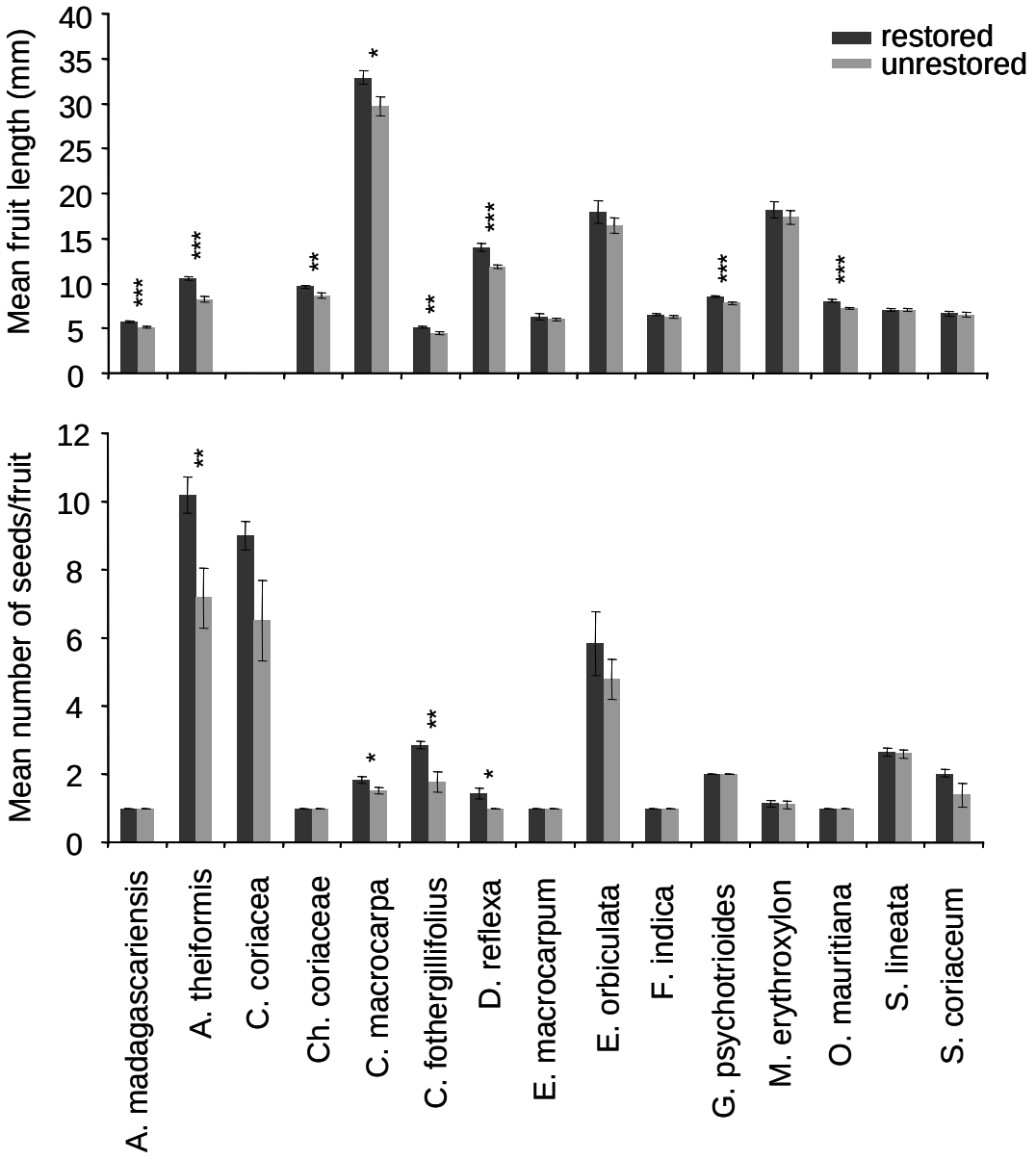

Figure 6 Differences in fruit size (mm) and mean number of seeds per fruit for 15 common plant species between the restored and the unrestored site. Fruit length was analysed with student's *t*-tests for each species (with sequential Bonferroni correction), and mean number of seeds per fruit with Mann-Whitney *U*-test. Level of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

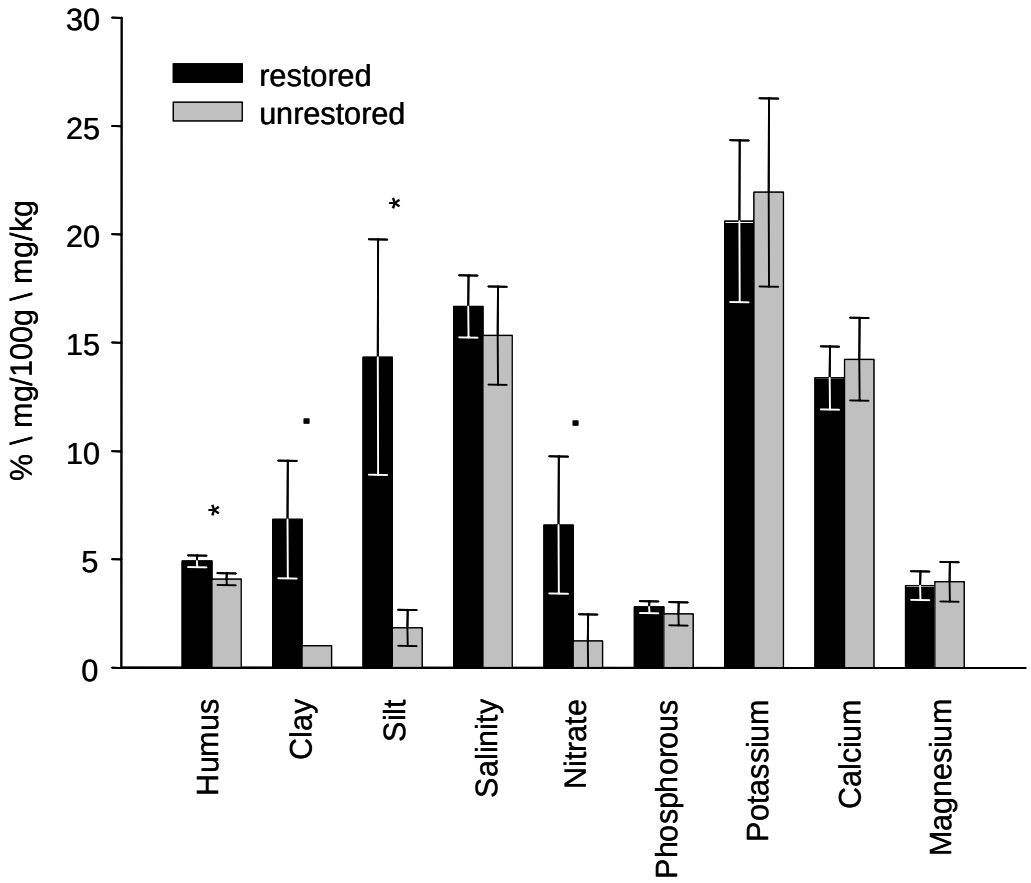

Figure 7 Mean composition and nutrient content of soil from the restored and the unrestored site. Humus, clay and silt were measure in percent, salinity was expressed in mg/100g and the unit of all five soil nutrients was mg/kg. Error bars denote standard error. Humus (Mann–Whitney $U = 6.0$, $p = 0.045$) and silt ($U = 4.5$, $p = 0.026$) were significantly higher in the restored site, and clay ($U = 9.0$, $p = 0.058$) and nitrate ($U = 7.5$, $p = 0.078$) content were marginally higher in the restored site. p-values: . < 0.1, * < 0.05.

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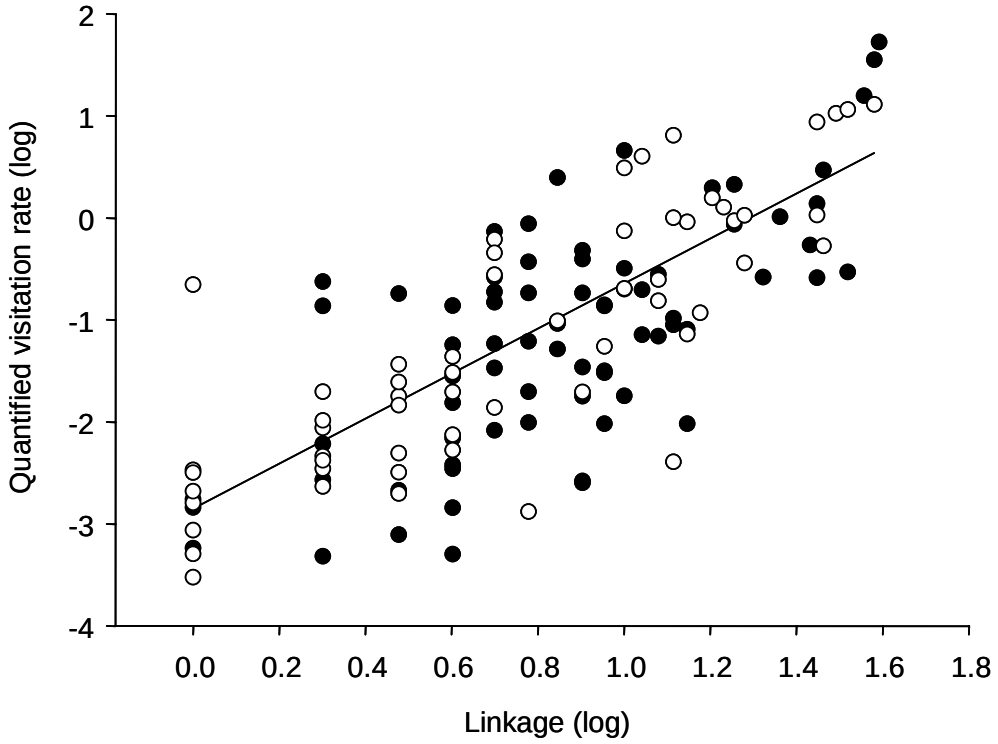

Figure 8 Log-log relationship between quantified visitation rate of each plant species and linkage level in the restored (full circles) and the unrestored site (empty circles).

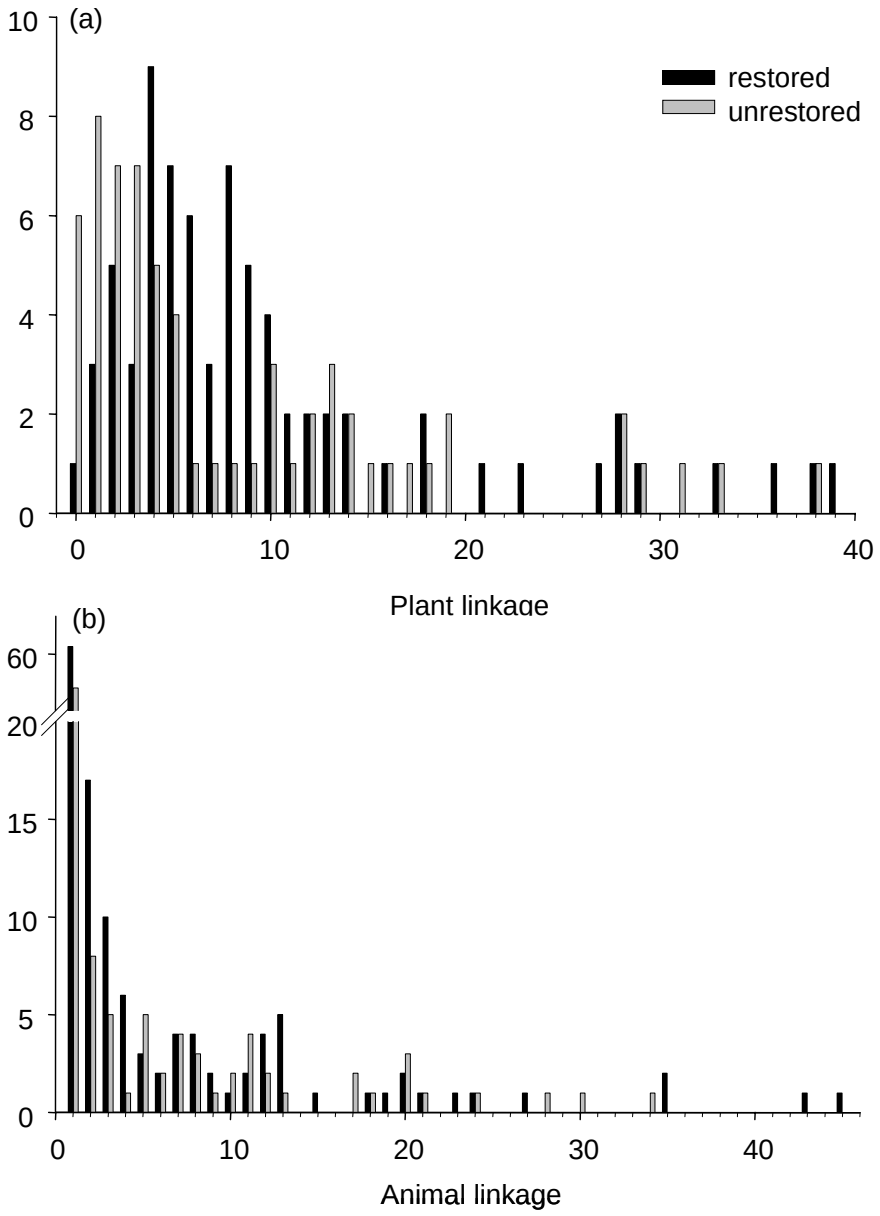

Figure 9 Frequency of (a) plant linkage and (b) pollinator linkage in the restored and the unrestored site. Each bar represents the count of species with a given linkage (number of taxa interacted with). The majority of pollinator species visited only one plant species, and few pollinators were extremely generalised. Pollinator species with a low linkage are less likely to be observed than species with a higher linkage. Species identity is given for highly generalised plant species: 1. *Sideroxylon cinereum*, 2. *Sideroxylon puberlum*, 3. *Stillingia lineata*, 4. *Psidia terebinthina* (both restored and unrestored), 5. *Aphloia theiformis*; animal species: 6. *Stomorhina lunata*, 7. *Chaetocnema* sp., 8. *Pachycerina crinicornis*, 9. *Apis mellifera*, 10. *Technomyrmex albipes*.

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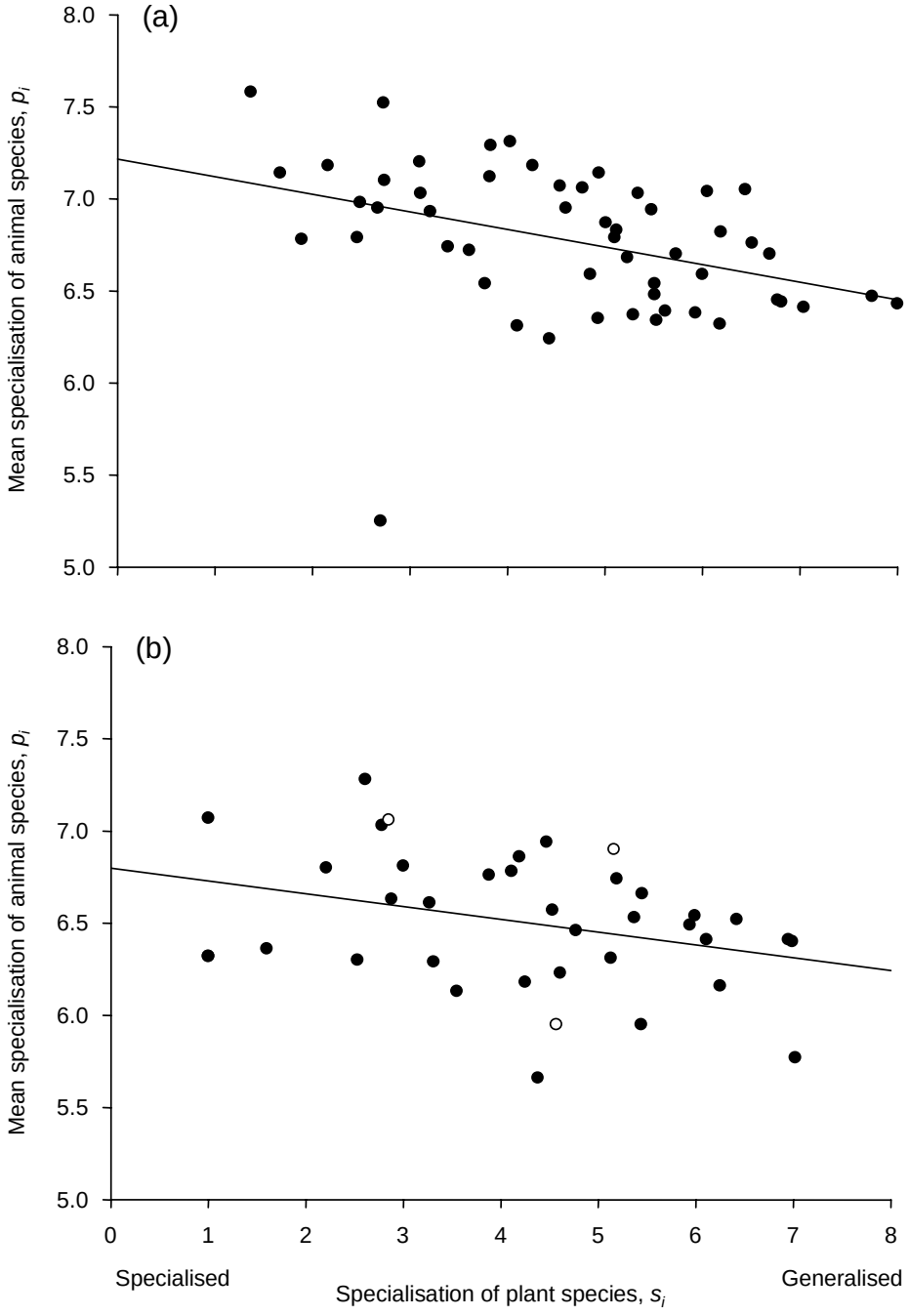

Figure 10 The relationship between degree of specialisation of plant species (s_i, the higher the number, the more generalised the species) and the mean specialisation index of their flower visitors (p_i) in (a) the CMA and (b) the unrestored site. Empty circles in (b) represent the three introduced plant species in the community which received enough visitors to be included in this statistics.

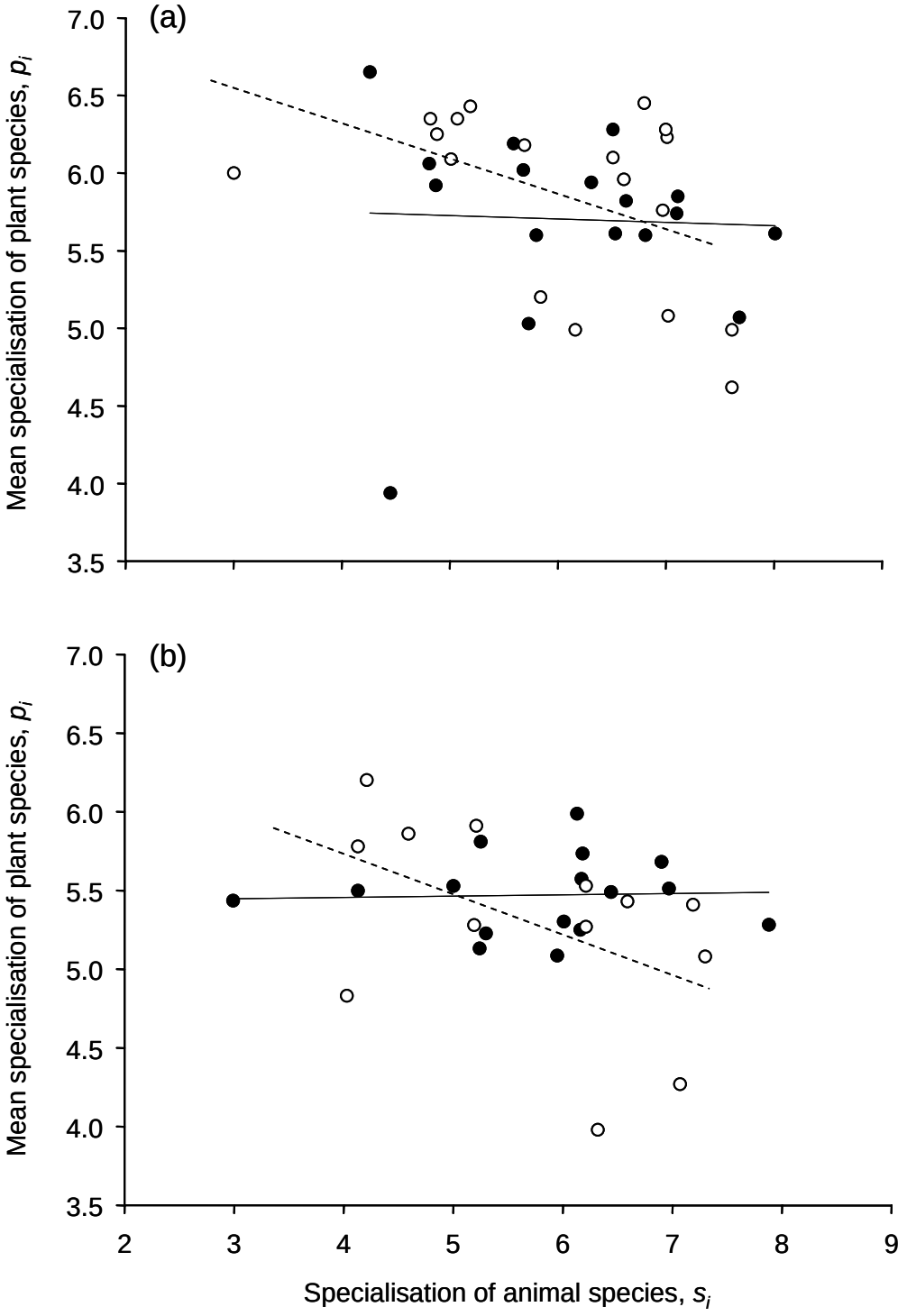

Figure 11 The relationship between degree of specialisation of animal species (s_i) and the mean specialisation index of the plants they visit (p_i) in (a) the CMA and (b) the unrestored site. Full circles depict native pollinators and empty circles show introduced pollinators. Lines of best fit are depicted for native (solid) and introduced (dotted) pollinators separately.

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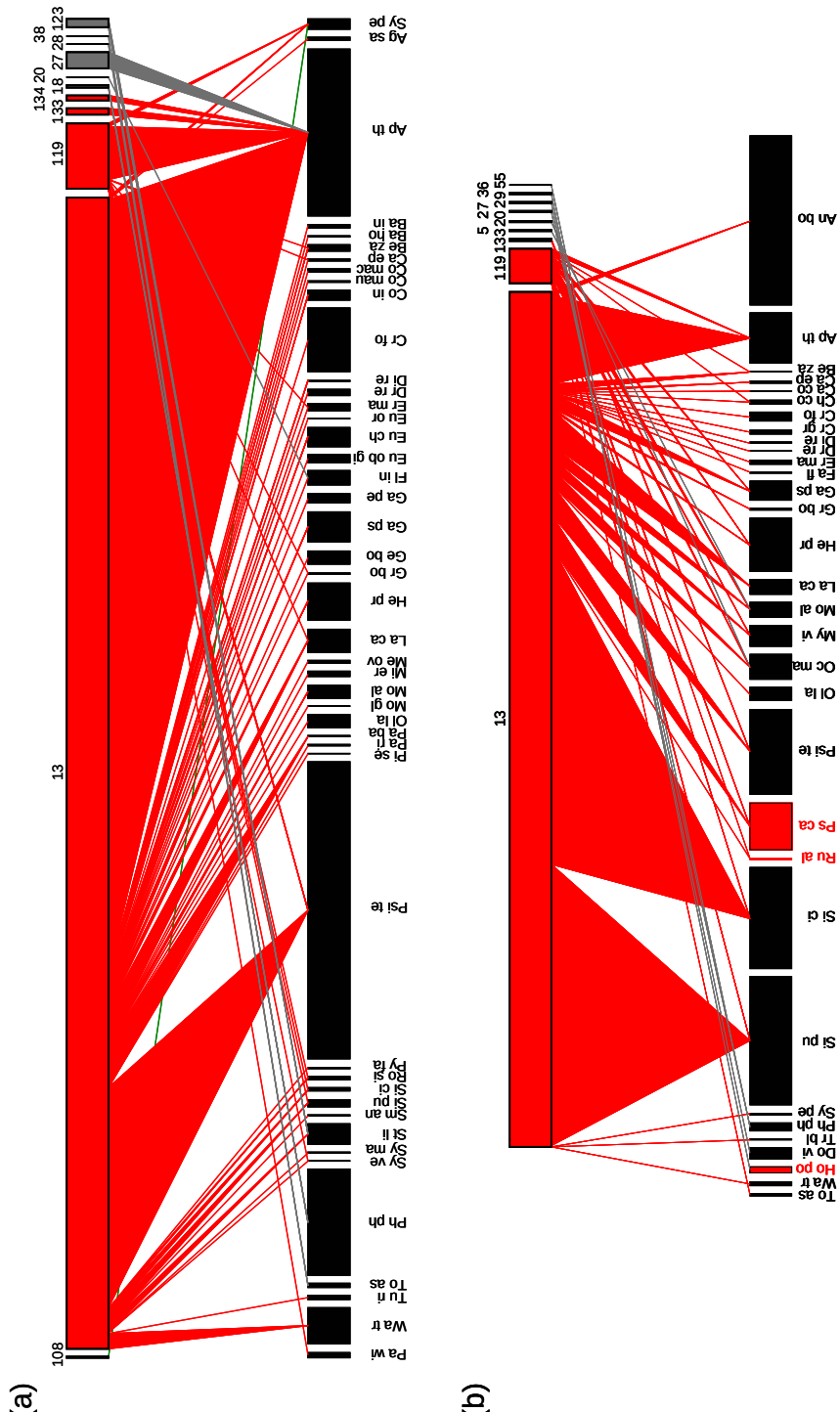

Figure 12 Quantified visitation webs for plants and Hymenoptera pollinator (excluding Formicidae) in (a) the restored and (b) the unrestored site. Visitor species are shown as rectangles at the top and plant species are shown at the bottom. The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantified visitation rate between an interacting pair of species. Webs are drawn to the same scale. Colours represent the origin of animal species; green: native; red: introduced; grey: unknown. Plant species highlighted in red are introduced. For plant and animal codes see Appendices III & IV. 13 = *Apis mellifera* (honey bee).

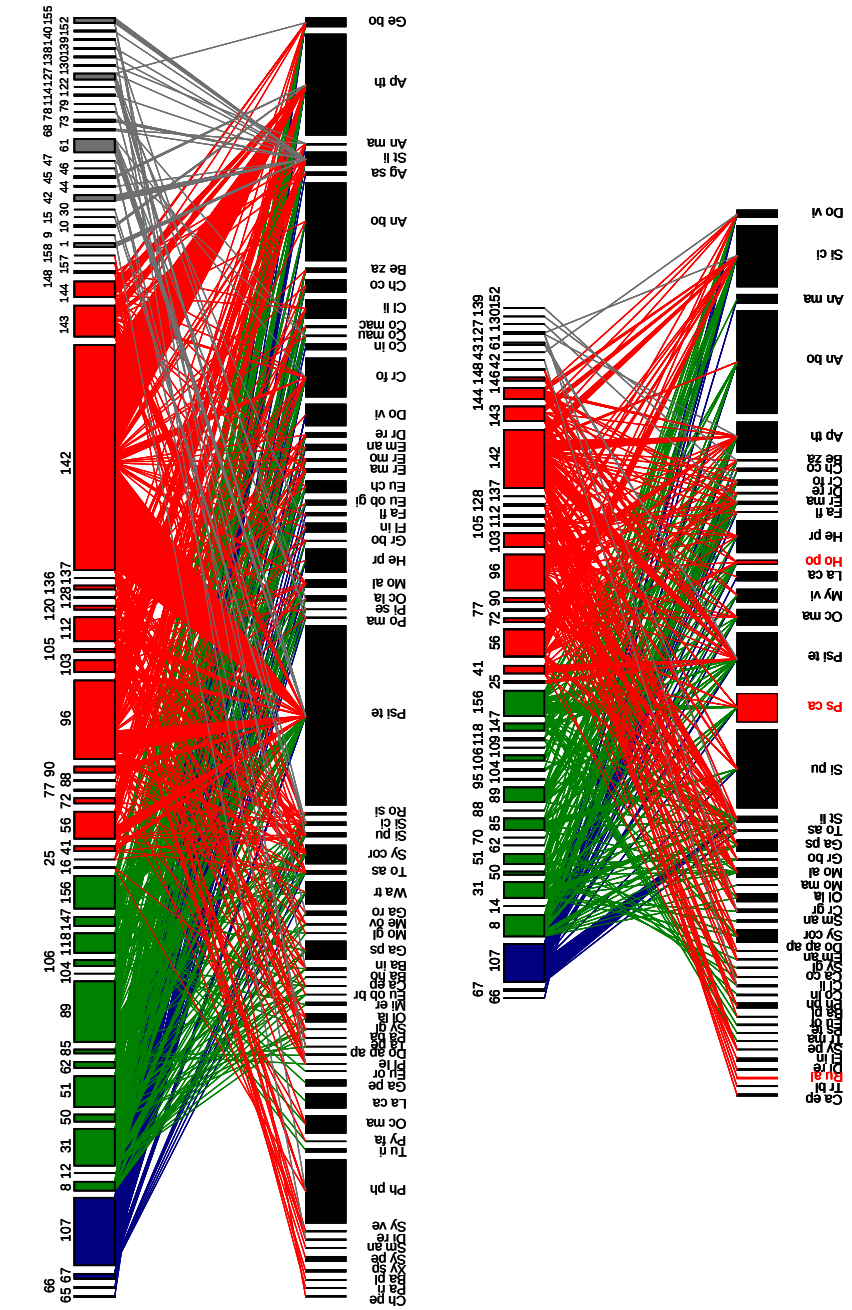

Figure 13 Quantified visitation webs for plants and dipteran pollinator in (a) the restored and (b) the unrestored site. Visitor species are shown as rectangles at the top and plant species are shown at the bottom. The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantified visitation rate between an interacting pair of species. Webs are drawn to the same scale. Colours represent the origin of animal species; blue: endemic; green: native; red: introduced; grey: unknown. Plant species highlighted in red are introduced. For plant and animal codes see Appendices III & IV.

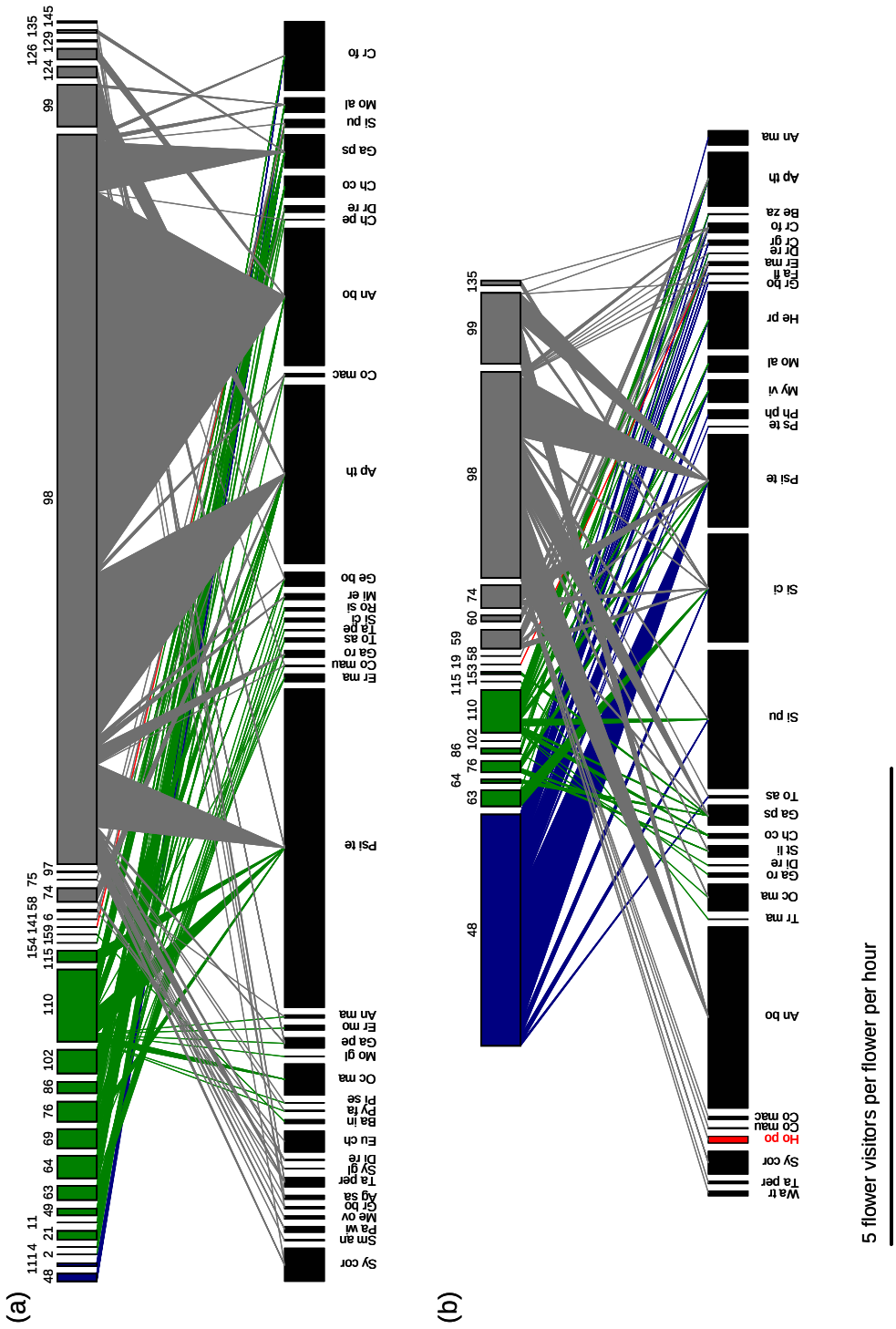

Figure 14 Quantified visitation webs for plants and lepidopteran pollinator in (a) the restored and (b) the unrestored site. Visitor species are shown as rectangles at the top and plant species are shown at the bottom. The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantified visitation rate between an interacting pair of species. Webs are drawn to the same scale. Colours represent the origin of animal species; blue: endemic; green: native; red: introduced; grey: unknown. Plant species highlighted in red are introduced. For plant and animal codes see Appendices III & IV. 48 = *Dysauxes florida*; 98 = *Nacoleia* sp1

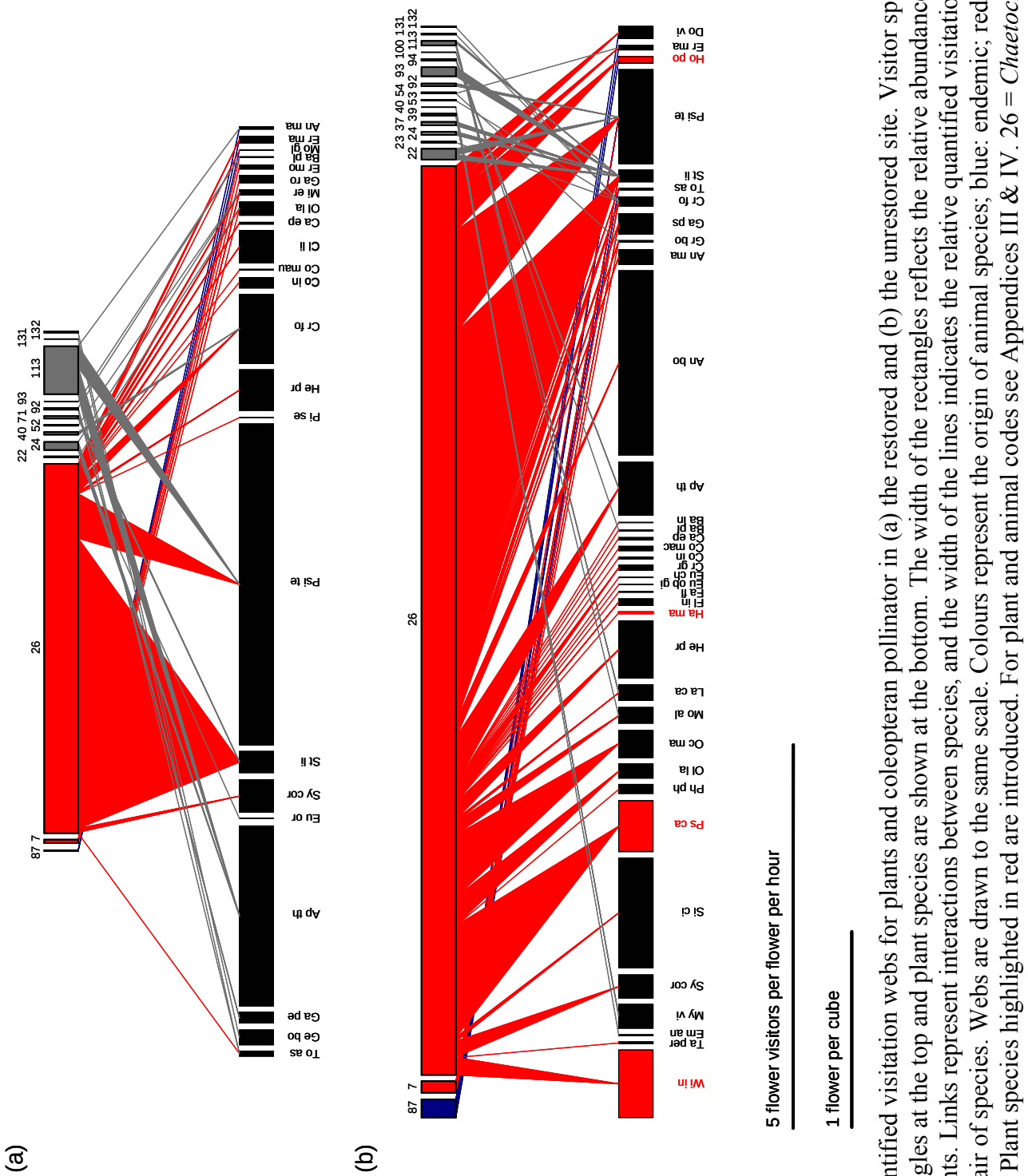

Figure 15 Quantified visitation webs for plants and coleopteran pollinator in (a) the restored and (b) the unrestored site. Visitor species are shown as rectangles at the top and plant species are shown at the bottom. The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantified visitation rate between an interacting pair of species. Webs are drawn to the same scale. Colours represent the origin of animal species; blue: endemic; red: introduced; grey: unknown. Plant species highlighted in red are introduced. For plant and animal codes see Appendices III & IV. 26 = *Chaetocnema* sp

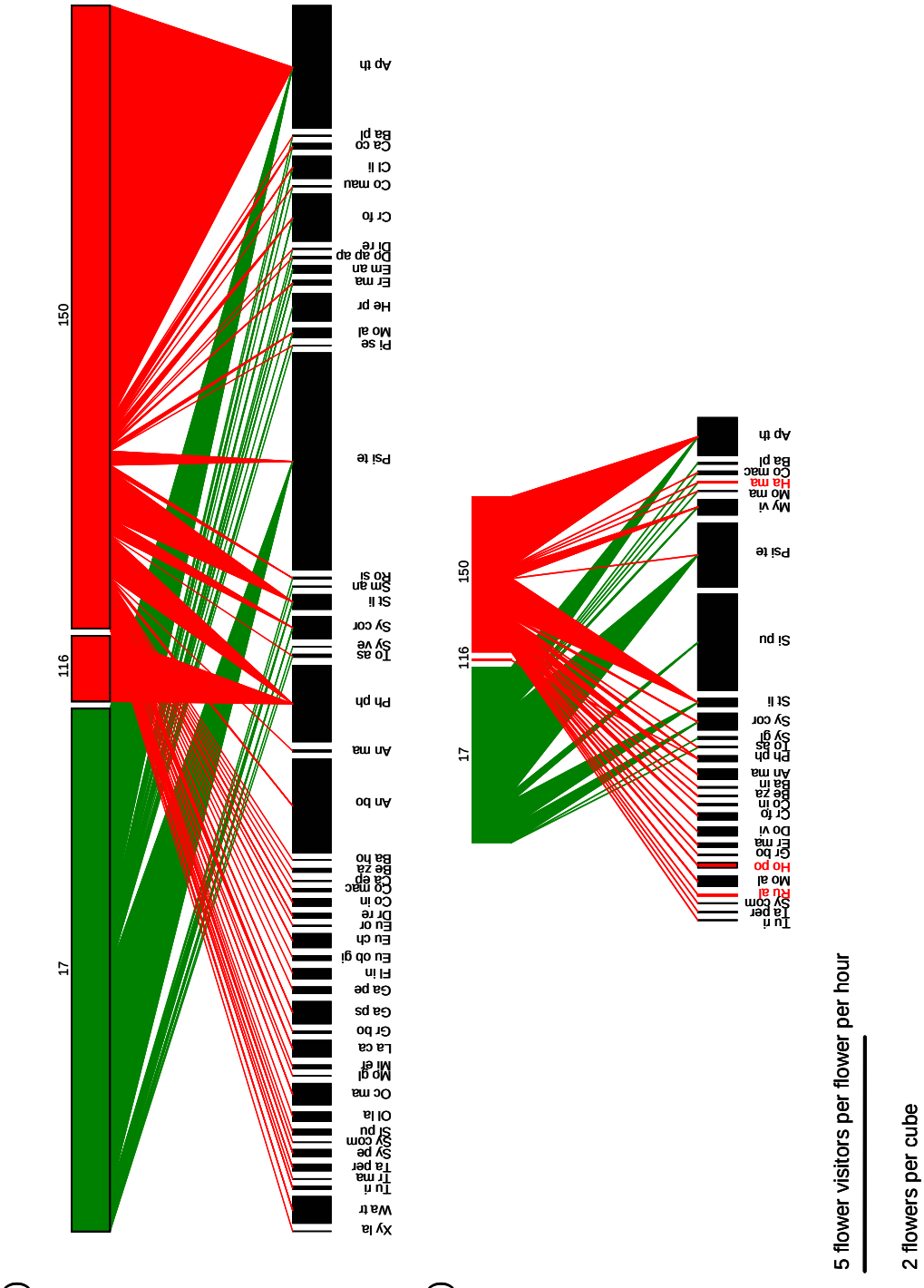

Figure 16 Quantified visitation webs for plants and ant pollinators (Formicidae) in (a) the restored and (b) the unrestored site. Visitor species are shown as rectangles at the top and plant species are shown at the bottom. The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantified visitation rate between an interacting pair of species. Webs are drawn to the same scale. Colours represent the origin of animal species; green: native; red: introduced; Plant species highlighted in red are introduced. For plant and animal codes see Appendices III & IV.

CHAPTER 7

Temporal dynamics in plant–pollinator network structure

Christopher N. Kaiser, Jane Memmott and Christine B. Müller

(to be submitted to *Ecology Letters*)

ABSTRACT

Network topology has implications for the stability and the resilience of these networks to perturbations. We compared flower visitation webs for 13 consecutive fortnightly periods from a restored and an unrestored site. The network properties connectance, degree distribution and nestedness were used to describe temporal and spatial variation in plant–pollinator systems and network topology. We found large fluctuations in species diversity (i.e. network size), floral and pollinator abundance between fortnights and sites. Connectance was lowest and nestedness was highest during the peak flowering period, whereas the degree distribution, despite showing temporal variation, indicated no such pattern. Networks covering the entire study season were best described by a truncated power-law degree distribution, and most temporal networks also showed truncated power-law or exponential decays of the degree distribution. Network properties also varied between sites, with lower connectance at the restored site and more exponential degree distributions of the animal communities in the unrestored site. These findings show that network structure and, thus, network stability and complexity, are not static throughout the season. This has implications for those animal and plant species which are phenologically constrained to parts of the season when network stability is low, increasing their susceptibility to disturbance. Such temporal fluctuations in network properties should be taken into account in future network studies.

INTRODUCTION

In the search for underlying mechanisms describing regularities in network topology, ecologists have studied a wide range of biotic networks including mutualistic networks between plant and pollinators or plant and seed dispersers. Such bipartite networks depict interactions (links) between mutualistic species (nodes), and quantitative data on the frequency of visitations between two interaction partners can be visualised with plant–pollinator webs (Memmott 1999; Chapter 6). Beyond patterns of abundance and species richness, several approaches developed in physics, economics and the social sciences have been applied to the analysis of plant–animal interaction networks (Strogatz 2001, Newman *et al.* 2002, Bascompte *et al.* 2003). Explaining the inherent structure of complex networks is of central importance for understanding network functions (Pimm 1984), and there are three salient properties describing network topology; 1) connectance; 2) distribution of the number of links per species (degree distribution) and; 3) interactions structure. One of the patterns describing interaction structure is nestedness (Lewinsohn *et al.* 2006).

1) Connectance is the ratio of observed interspecific interactions to the number of possible interactions in a network, and thereby it is a direct measure of network complexity and a core element of the complexity-stability debate (May 1972, Pimm 1984). In contrast to scale-invariant network properties, which remain constant across webs of different types and sizes (Briand & Cohen 1984, Sugihara *et al.* 1989), connectance is scale-dependent (or broad-scale invariant), showing a negative, hyperbolic relationship with network size (e.g. Jordano 1987, Petanidou & Potts 2006). Most plant–pollinator networks are sparsely connected, since many interactions are simply not observed or only a small fraction of the total possible interactions actually occurs (Jordano *et al.* 2006). Thus, connectance can vary widely among plant–pollinator networks (see Olesen & Jordano 2002). This variation may partly be due to the scale-dependency of connectance, and due to a bias created by sampling effort (Goldwasser & Roughgarden 1997, Bersier *et al.* 1999).

2) Degree distributions reveal patterns in the structure of networks, which have implications for the stability and the resilience to perturbations of these networks (Barabási & Albert 1999). For example, complex networks have been shown to grow following preferential attachment (Barabási & Albert 1999, Newman 2003), whereby new species joining the network preferentially interact with highly connected (generalised) species, which can be illustrated by a degree distribution following a power-law function. Most mutualistic networks, however, depart from this scale-free degree distribution and decay faster than expected under a power law (Jordano *et al.* 2003). Truncated power-law distributions have a

bulk of species with few interactions and a tail which deviates (sometimes exponentially) from the power-law function, whereas exponential degree distributions characterise randomly assembled networks. Jordano *et al.* (2003) suggested that "forbidden links" (non-matching phenotypes or non-overlapping phenologies between interaction partners) impose a constraint on network growth by limiting the number of possible interactions per species, which would explain the more rapid decline of the tail of the degree distribution than under a power-law (see also Waser *et al.* 1996, but see Vazquez 2005).

3) A third approach to investigate structural organisation of mutualistic networks is the concept of nestedness. An interaction matrix (plants × animals) sorted in descending order by level of generalisation (from most generalised to most specialised species) is described as perfectly nested when each species interacts only with a proper subset of those species interacting with more generalised species (Bascompte *et al.* 2003). The result would be a highly cohesive community where generalist pollinators interact with their generalised counterparts generating a stable core of interactions. In contrast, if plants and pollinators are highly specialised and each species has only one mutualistic partner, the network would show anti-nestedness (Poulin & Guegan 2000, Dupont *et al.* 2003). Both conditions of nestedness describe a non-random pattern of network structure which may have implications for co-evolutionary interactions in diverse communities, for rare species persistence, and the system response to perturbations (Bascompte *et al.* 2003).

Although many studies have contributed to our knowledge on the structure of complex networks during the last few years, little is known about how these patterns change over time. Despite remarkable recent achievements in collecting large and highly resolved plant–pollinator networks, most studies pool information on species and interactions over the entire study period, and thereby may also mask temporal alterations in network structure. Olesen and Jordano (2002) highlighted that the lack of temporal resolution is a serious drawback in the analysis of mutualistic networks and that the role of a temporal component in network studies is often overlooked. To date, studies have presented network properties which describe static systems from either a single season or data pooled over several years (but see Medan *et al.* 2006). However, plant–pollinator communities are subject to continuous spatial and temporal change in species composition, which is likely to influence inherent network structure.

Here, we present 13 pairs of fully quantified visitation webs from consecutive fortnights for the period August 2003 to March 2004. Each pair consists of one web from a site undergoing restoration and one from an adjacent unrestored site in Mauritius. We

investigate how the three network properties connectance, degree distribution and nestedness change over the flowering season. Plant–pollinator network growth is particularly strong at the beginning of the season and after abiotic disturbances, e.g. cyclones (here in December, January). We predict that fortnightly networks show power-law degree distributions at times when network growth is high and new species are added to the networks frequently due to preferential attachment (Barabási & Albert 1999, Amaral *et al.* 2000).

We address the following questions: (1) How do quantified fortnightly visitation webs change throughout the season? (2) How do the three network properties connectance, degree distribution and nestedness change over time? (3) Are there differences in (1) and (2) between the restored and the unrestored site?

MATERIALS AND METHODS

Study sites

The study was carried out at Pétrin (20°40' S, 57°46' E, 670 m a.s.l.), within the Black River Gorges National Park, Mauritius. The prevailing vegetation type of Pétrin is the formerly widespread *Erica/Phylica*-heath, which is characterised by low growth, high plant diversity and a relatively clumped distribution of plants interspersed with patches of bare soil (for a detailed description of the habitat see Chapter 6). The native vegetation in this area is largely degraded following heavy invasion by introduced plant species. To restore parts of the native habitat, the governmental National Parks and Conservation Service (NPCS) and the Mauritian Wildlife Foundation (MWF) have established Conservation Management Areas (CMA) in all major habitat types. Each CMA is fenced and invasive plant species are eradicated by hand-weeding. The study sites were two plots of equal size (330 × 100 m), one of which was located within the CMA in Pétrin (hereafter "restored site"), and the second (hereafter "unrestored site") was set up at a distance > 500 m from the restored site in a degraded area with a similar native plant species composition to the CMA. Invasive alien plant species have altered the plant community structure in the unrestored site so that, in parts, the introduced strawberry guava *Psidium cattleianum* formed dense stands depriving the vegetation of its originally semi-open structure.

Visitation webs

The general framework within which the data collection for the visitation webs was conducted is described in Chapter 6. Here, we focus mainly on the fortnightly plant–pollinator networks (in contrast to the overall, seasonal networks) sampled throughout the field period

between calendar week 37 (starting 15th September 2003) and week 9 (starting 15th March 2004), a total of 13 networks at each site (for sampling techniques see Chapter 6). Flower counts were conducted fortnightly, providing the data on floral abundance of each visitation web. Due to the low density of individuals of some rare plant species, one or two flowering species each fortnight were not included in the random counts of a given fortnight. For these species, floral abundance was calculated based on average counts from the previous or following fortnight. All flowering plant species were observed for animal visitors for a total of 2 h (4 × 30 min) per species and site in each fortnight period. Visitation rate was defined as the number of visits flower^{-1} hour^{-1}, and quantified visitation rate was calculated by multiplying visitation rate by the fortnightly floral abundance of the visited plant species (see Chapter 6). To investigate temporal variation in network size, we analysed the relationship between total floral abundance (explanatory variable) and total pollinator abundance (i.e. sum of quantified visitation rate; response variable) across fortnightly networks with a linear model. 'Site' (restored/unrestored) was fitted first into the model to account for dependencies between networks at the same site.

Network properties

We analysed three network parameters to investigate how network topology changed over time.

Connectance

Network connectance is defined as the fraction of observed interactions over the total number of possible interactions; $C = 100 \times (I/P \times A)$ where I is the total number of interactions observed and P and A are the numbers of flowering plant and animal species, respectively. Connectance was calculated for each fortnightly network. We compared mean network connectance between sites across fortnights with a paired *t*-test. We tested the relationship between connectance and network size with a linear model, controlling for site dependencies by entering site first into the model.

Degree

Degree describes the number of interactions per species. In chapter 6, we used the term linkage, which is synonymous with degree and frequently used with respect to visitation webs. Here, we used the term degree, k, to maintain consistency with recent research on complex network topology (e.g. Strogatz 2001). Variation in mean degree of animal and

plants across networks was analysed with a linear mixed effects model, controlling for within-group effects by fitting 'Site' (restored/unrestored) as random factor. One important parameter defining network properties is network size. The relationship between degree and network size was analysed with a linear model. We are aware of the temporal pseudoreplication in the analysis which increases the likelihood of committing too many Type I errors. To remove the dependence among the within-group errors, we entered 'Fortnight' (continuous) and 'Site' first into the model (Crawley 2003). Degree was $\log_{10}$-transformed to reach normality and homoscedasticity of the residuals.

In addition to presenting mean degree of animal and plant species for each network, we examined the cumulative distribution P(k) of the number of interactions per species, k (called connectivity or degree distribution). We fitted three different models: (1) exponential, $P(k) \sim \exp(-\gamma k)$; (2) power-law $P(k) \sim k^{-\gamma}$; and (3) truncated power-law model, $P(k) \sim k^{-\gamma} \exp(-k/k_x)$, where k is the degree, γ is the fitted constant and k_x is the truncation value (Jordano *et al.* 2003). The truncation value is the critical point when the recorded degree diverts from the power-law distribution and thereby decays faster then expected from a power-law function. To evaluate the effect of the tail of the degree distribution on the power-law behaviour for small networks (fortnightly networks), we computed the power-law exponent of P(k) only using the first five observed values of k (Guimarães *et al.* 2005). The tail effect was reduced in the overall, seasonal networks so that we calculated the power-law model for the entire observed distribution. We fitted the degree distribution models to the data with the non-linear regression (nls) function in the statistic package R 2.2.1 (R Development Core Team 2005). The model fit was assessed by Akaike Information Criterion (AIC; Akaike 1974). Earlier studies compared ANOVA statistics (e.g. *F* values) or the adjusted R^2 values to find the best fit to the different models (e.g. Jordano *et al.* 2003). However, these statistics would assume orthogonality among components of the residual vector, which is unlikely to occur in non-linear relationships (D. Bates, R help, https://stat.ethz.ch/pipermail/r-help/2000-August/007778.html, 12th August 2000).

To investigate the relationship between the best model fit of the degree distribution and network parameters such as network size and mean degree, we computed generalised linear mixed-effects model with penalised quasi-likelihood (hereafter GLMM) (glmmPQL function in R.2.2.1, using the MASS library; Breslow & Clayton 1993, Venables & Ripley 2002). We conducted one analysis for each of the three models and the binary response variable was coded 1 = best fit and 0 = not fitted. The full model contained the explanatory variables network size, squared network size, mean degree, taxon (plant/animals), site

(restored/unrestored) and fortnight. A combined site/taxon variable was entered as random variable in the model. The full model was simplified step-wise by using AIC, and only the minimum adequate model is presented here. Similarly, we investigated the relationship between the fitted constant γ of all three models and network size with linear mixed effects models. Absolute γ-values were log-transformed to reach the assumptions of normality and the same variables as in the GLMM were included in the model.

Nestedness

A binary matrix contains presence/absence data of interactions between a plant (*P*) and an animal species (*A*), where one cell in the matrix depicts a 1 if *P* and *A* interact, and zero otherwise. Originally derived from the analysis of species occurrence patterns on islands or habitat fragments (Patterson & Atmar 1986, Atmar & Patterson 1993, Lomolino 1996), nestedness in plant–animal networks adopts a logically closely related concept. Pollination networks are perfectly nested if the most specialised animals use food plants which are perfect subsets of those used by more generalised animals. In return, interactions of the most specialised plant species are a proper subset of the more generalised interactions between plants and their pollinators. We used the programme 'Nestedness Temperature Calculator (NTC)' (Atmar & Patterson 1995) to calculate a measure of nestedness, called temperature (*T*). To assess the statistical significance of nestedness, we compared the observed *T* value to a benchmark provided by a null model. We used the simple null model by Patterson and Atmar (1986) which generates random networks of similar size constraining only the total number of interactions in the system. The null model used by the NTC was shown to potentially overestimate nestedness and its statistical significance (Fischer & Lindenmayer 2002), so we used three other null models calculated by the programme ANINHADO (Guimarães & Guimarães in press) to test the reliability of the NTC model. Significance status did not change between models, and we will present the results from the NTC model throughout the paper. Network *T* was statistically tested using Monte Carlo simulations based on 1000 randomisations. Instead of using network temperature which is a measure of disorder, we defined matrix nestedness (*N*) as $N = (100 - T)/100$, with 1 being maximally nested. To compare nestedness across fortnightly networks, we calculated relative nestedness $N^* = (N - N_r)/N_r$, where *N* is the matrix nestedness and N_r is the average nestedness of the Monte Carlo randomizations (Bascompte *et al.* 2003).

RESULTS

Visitation webs

Quantified visitation webs of the 13 fortnightly plant–pollinator communities showed high temporal and spatial variation in species richness and abundance (Fig. 1; for species identities see Appendix VIII). The restored and the unrestored community were most species-rich at the beginning of November and the end of October respectively, and most species-poor in March and at the beginning of January, respectively (Table 1). The ratio of plant to animal species in the networks fluctuated between three times more animal species at the beginning of the flowering season and twice as many plant as pollinator species in December (unrestored). The sizes of the visitation webs varied by a factor of 50 in terms of pollinator visitation and by a factor of 17 in terms of floral abundance. Based on quantified visitation rate, the majority of visitation webs were, at least three times larger in the restored than in the unrestored site (fortnights 1, 2, 4, 8, 9, 11 & 12) and only one web (fortnight 3) was 30% larger in the unrestored site. During fortnight 3, the endemic *Sideroxylon cinereum* (Sapotaceae) provided a highly abundant floral resource in the unrestored site (70% of total floral abundance) resulting in 58.8% of all visits during this period. Of all visits to *S. cinereum*, 85% were carried out by three introduced pollinator species (*Apis mellifera* (Apidae)*, Stomorhina lunata* (Calliphoridae) and *Fannia pusio* (Fanniidae); see also Chapter 6), most of which visited *S. cinereum* exclusively (Appendix VIII). Once *S. cinereum* stopped flowering (fortnight 4), highly abundant pollinators disappeared from the webs. *Sideroxylon cinereum* did not flower during the same fortnight in the restored site. Visitation webs of fortnights 5, 6, and 7 were similar between sites, marking a continuous period of high floral and pollinator abundance. Although total pollinator activity corresponded closely with total floral abundance ($R^2 = 0.31$, $F_{1,22} = 11.1$, $p = 0.003$), a few visitation webs deviated from the observed pattern. The overall observed ratio of pollinator abundance to floral abundance was approximately 3:1. In fortnight 3, the total number of visits exceeded floral abundance by a factor of 6 in the restored and 8 in the unrestored site, and in fortnight 7, the ratio was 1:1 in the restored and 2:1 in the unrestored site.

Different pollinator taxa were most active at different times of the flowering season. At the restored site, for example, lepidopteran species diversity and relative abundance were highest from the end of October (fortnight 4) to the beginning of December (fortnight 6). Hymenoptera (mainly the introduced honey bee *Apis mellifera;* excluding Formicidae) were most abundant at the beginning of October (fortnight 3) and in December (fortnights 7 & 8), whereas the relative abundance of hymenopterans at one site was not directly linked to the

occurrence at the other site (e.g. fortnight 6). The blue-tailed day gecko *Phelsuma cepediana* was mostly observed during the second half of the season, both with increasing abundance and increasing number of plant species visited. At the unrestored site, the relative abundance of Coleoptera (mainly the introduced flea beetle *Chaetocnema* sp.) was highest during October, November and February (fortnights 4, 5, 6, 10) and lowest in January and at the end and the beginning of the season (fortnights 1, 8, 9, 12, 13). However, in almost all months, beetle diversity and abundance was higher in the unrestored than in the restored site. Dipterans were most diverse and abundant at both sites, but species distributions varied greatly among fortnights. In the unrestored site, there appeared to be a trade-off between dipteran species richness and abundance; during fortnight 3 and 7 the dipteran pollinator communities consisted of a few highly abundant species, and the other webs showed similar abundance of most dipteran species.

Connectance

Network connectance at the restored site was highest in October ($C = 22.2$, fortnight 3) and lowest at the end of November ($C = 6.7$, fortnight 6). At the unrestored site, the networks were most connected in October ($C = 25.3$, fortnight 3) and least connected at the end of February ($C = 10.1$, fortnight 12; Table 1). Although most networks were more connected in the unrestored site (except fortnights 1 and 13), mean connectance was only marginally significantly different between sites (paired $t = –1.98$, $p = 0.071$, $df = 12$). Throughout November to January, connectance in the restored site was lower than the least well connected network in the unrestored site. There was a trend towards connectance being negatively related to network size ($F_{1,22} = 3.32$, $p = 0.081$) and this relationship did not differ between sites (site × size: $F_{1,22} = 2.54$, $p = 0.12$).

Degree

Mean pollinator and plant degree varied significantly over time, with pollinator degree showing relatively small variation of 2.0 compared to plant degree, which showed a maximum range of 8.3 (k_{animal}: $F_{1,23} = 8.42$, $p = 0.008$; k_{plant}: $F_{1,23} = 37.1$, $p < 0.0001$), but there was no difference in mean degree between sites (k_{animal} paired $t = 0.06$, $p = 0.95$, $df = 12$; k_{plant} paired $t = 0.64$, $p = 0.53$, $df = 12$; Table 1). Plants interacted on average with more pollinator species than *vice versa* (mean k_{plant}: 4.66 ± 0.48; mean k_{animal}: 2.38 ± 0.10; paired $t = 5.12$, $p < 0.0001$, $df = 25$). In the unrestored area, there was a trend towards degree being positively related to network size (Fig. 2; site × network size $F_{1,21} = 4.06$, $p = 0.057$). The

truncated power-law model showed the best fit to the degree distribution of three out of four plant–pollinator networks which covered the entire study period (animal and plants fitted separately, Table 2). Only the plant community in the restored site showed the best model-fit to the exponential degree distribution (Fig. 3). Most degree distributions of fortnightly plant and pollinator communities showed best model fits to exponential or truncated power-laws (Table 3, Appendix IX). Power-law best fits were rare in animal communities and absent in plant communities, which is expected for relatively small networks because degree distributions show a power-law only in networks with a relatively large number of species. The γ exponent for the power-law fits was significantly higher for animal than for plant communities (γ_{animal}: 1.19 ± 0.04; γ_{animal}: 0.69 ± 0.03; paired $t = 7.85$, $p < 0.0001$, $df = 25$), which was also recorded by Jordano *et al.* (2003). The frequency of best model-fits to degree distributions of fortnightly pollinator and plant communities differed from random (pollinator: $\chi^2 = 9.54$, $p = 0.008$, $df = 2$; plant: $\chi^2 = 15.4$, $p < 0.0001$, $df = 2$). Best model fits of the degree distribution of fortnightly networks were not related to any of the explanatory variables (Table 4), with exception of power-law fits, which were related to low mean degree coupled with large network size (squared).

Nestedness

Overall plant–pollinator networks for the entire season were highly nested (restored: $N = 0.949$, $p < 0.0001$; unrestored: $N = 0.959$, $p < 0.0001$), with the network at the restored site showing higher relative nestedness than expected from random compared to the network at the unrestored site ($N_r = 0.43$ *vs* 0.36). Mean nestedness across sites increased from fortnight 1 (September), peaked in fortnights 6 and 7 (November/December) and showed a steep decline after fortnight 10 (end January; Fig. 4a). The average nestedness of fortnightly networks did not differ between sites (restored: 0.828 ± 0.02; unrestored: 0.831 ± 0.02 paired $t = 0.25$, $p = 0.81$, $df = 10$; only significantly nested networks included, see Table 1), but when accounting for species richness and the number of interactions, mean relative nestedness was higher in the unrestored than in the restored site (restored: 0.25 ± 0.05; unrestored: 0.35 ± 0.03 paired $t = -3.04$, $p = 0.012$, $df = 10$). Relative nestedness also varied over time between sites (Fig. 4b). At the beginning of the season, both networks appeared highly nested. After fortnight 3, relative nestedness dropped sharply at the restored site and, despite a decline of relative nestedness in the unrestored site at the same time, the networks in the restored site maintained lower relative nestedness throughout the season than the network in the unrestored

site. After removing dependencies between spatial and temporal variation, nestedness showed a positive linear relationship with network size ($F_{1,20} = 5.71$, $p = 0.026$).

DISCUSSION

Plant–pollinator networks are everything but static systems with a single inherent structure throughout the season. We found large fluctuations in species diversity (i.e. network size), floral and pollinator abundance, and in the three network properties among fortnightly networks. Overall, we reported highest connectance at the start and end of the field period as well as in January (in the middle of the flowering season), which corresponded closely to network size. Plant–pollinator communities in the unrestored site showed a trend towards higher connectance than networks in the restored site. Mean degree of plant species was twice that of pollinators, and degree distributions for plant and animal communities varied between time periods. Lastly, almost all temporal networks showed a relatively high level of nestedness (~68% – 94%), with networks at both sites becoming increasingly nested towards the middle of the season and less nested towards the end.

Temporal patterns in visitation web properties

We initially posed the question: how do visitation webs change throughout the season? Previous studies have shown that the diversity of pollinator assemblages can vary considerably between years (Herrera 1988, Petanidou & Ellis 1996), which suggests that annual changes in web structure do occur. However, our study is amongst the first to examine detailed changes in visitation web structure at regular time intervals within a year, and we show that both the size and complexity of webs can vary substantially within one flowering season. Temporal fluctuations of similar magnitude were shown from an arctic plant-pollinator network (Lundgren & Olesen 2005), but network size was largest early and late in the season in contrast to our study where peak activity occurred in the middle of the main flowering season. Another relationship that emerged was that pollinator abundance and activity varied over time according to floral abundance. This is more likely to be a reflection of displacement of pollinators than of actual size fluctuations in their populations (e.g. Herrera 1988). Both visitation webs of fortnight 3 (beginning of October) showed a marked increase in size and were the largest, in terms of pollinator activity, of all periods. In the unrestored site, this was partly due to the copious floral reward offered by one ‘magnet’ species, *Sideroxylon cinereum* over this period. The observed drop in size and complexity of plant–pollinator networks at both sites at the beginning of January (fortnight 9) coincided

with the end of a six-week drought followed by cyclonic rainfall over a one-week period. Despite such peaks and troughs in web size and pollinator activity, the middle of the season (particularly throughout November and December) was a relatively stable period. Clearly, seasonality is an important consideration when selecting a timeframe to collect data for visitation webs. Our research suggests that data collected at the zenith of flower and pollinator activity would produce the most representative web if sampling time is limited. In our system, the preferred sampling time is in the middle of the season but, for example, in alpine habitats it would be early in the flowering season (Arroyo *et al.* 1982, Inouye & Pyke 1988, Lundgren & Olesen 2005).

Connectance indicates the general level of network specialisation in a system (Petanidou & Potts 2006). In networks with a high degree of specialisation, species establish a narrow range of interactions and do not utilise the full range of potential links. In particular, during the peak flowering period (fortnights 5, 6 & 7), connectance was lower than in other periods. One possible explanation is the occurrence of rare pollinator species attracted by the high floral diversity during this period. Such rare pollinators are often highly specialised (see also Vazquez & Aizen 2003, 2006) and thereby contribute to the decrease in connectance. Our finding of a negative relationship between connectance and network size over time concurs with those of earlier studies, which have pooled networks from single time periods (e.g. Jordano 1987, Olesen & Jordano 2002). Due to the scale-dependent behaviour of connectance, however, its function as indicator for specialisation is questioned (see Chapter 6).

Of the three degree distribution models described in the introduction, the truncated power-law describes communities where a large number of species has relatively few interactions and a small number of species interacts more frequently than expected by random, so-called 'super-generalists'. This model was the best fit to three of our four overall networks (plants and pollinators networks at two sites), with only the network for the restored plant community being best described by the exponential degree distribution, suggesting that the latter network was a more randomly built assemblage. Our prediction that, in times of network growth (beginning of the season and following disturbances), the power-law would fit best to the degree distribution was not supported by our data. In a power-law distribution, the mechanism of preferential attachment operates, decreasing the likelihood of the occurrence of super-generalists (Barabási & Albert 1999, Amaral *et al.* 2000). However, our data during the specified periods were best described by truncated power-laws, and animal communities in the restored site fitted best to power-law distributions throughout fortnights

5–8. This discrepancy with our prediction may be explained by the smaller network size at the beginning of the season (Keitt & Stanley 1998), the presence of highly connected cores in the networks (Guimarães *et al.* 2005) or by the presence of strongly operating 'forbidden links' (Jordano *et al.* 2003, Stang *et al.* 2006), which occur when there are limitations on the way species establish interactions. In addition, we found many degree distributions in plant communities declining exponentially, which suggest that the networks were assembled randomly. Hence, there may be few species-specific traits (e.g. phenological, physiological), which limit the possibility of a successful interaction. Morphological traits, however, may impose only a minimal constraint on interactions given that the most linked species have an open flower morphology, which allows access to most visitor species. Finally, we showed that mean and maximum plant degree were both higher than those for animals, which has also been recorded in Mediterranean communities (Petanidou & Potts 2006). This may partly be a consequence of our 'phytocentric' sampling bias (Jordano *et al.* 2006).

Highly nested networks show two important features; firstly, interactions are predominantly asymmetrical, i.e. generalists interacting with specialists, and secondly, nestedness implies that there is a cohesive 'nucleus' of interactions linking generalist plants with generalist pollinators. Thus, network stability emerges as a property of nestedness; nested systems are more robust and less vulnerable to perturbations. The core of interacting species may also allow more specialised interactions to persist (Bascompte *et al.* 2003). In our study, nestedness was highest in November/December, corresponding with the peak flowering period for most species, and also with network size. Throughout the study, and with the exception of the last two fortnights, networks appeared to be non-randomly assembled and showed relatively high nestedness values which lie within the range of that found in other pollination network studies covering single time points or pooled data over time (Bascompte *et al.* 2003, Dupont *et al.* 2003). The fact that two of our 13 temporal networks at each site were not nested emphasises the value of collecting data either at the peak of the flowering season or spanning the total flowering period.

Differences between sites

The visitation webs in the unrestored site were considerably smaller than those in the restored site. Pollinator abundance and activity was influenced by the presence or absence of super-abundant (1) generalist pollinators and (2) highly attractive floral resources of specific species. However, this pattern did not occur simultaneously at both sites (see also Chapter 6, Appendix VI). Such phenological uncoupling of plant species may reduce the effective

population size of a species in a given locality, which has implications for habitat restoration (Ghazoul 2005). Connectance varied between sites; the restored site showed lower overall connectance, which could indicate a higher availability of empty niches. Although we found no difference in mean degree between the restored and the unrestored site, the best model-fits to the degree distribution of animal communities appeared to vary between sites. In the unrestored site, animal degree distributions showed many more exponential fits than those in the restored site, implying that the former networks were generally more randomly assembled. Higher overall relative nestedness in the restored network suggests that this site had more interactions than expected compared to the unrestored site. However, given that we have investigated network properties of only one restored and one unrestored site, further studies are required to assess the implications of biological invasions on the topology of mutualistic networks.

In conclusion, we showed that general patterns in the way interactions are built in plant–pollinator communities fluctuate throughout the season. This has implications for those animal and plant species which are phenologically constrained to certain parts of the season when network stability is low, increasing their susceptibility to disturbance. The high degree of temporal variation in a range of network properties must be accounted for in the research of future network studies.

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Table 1 Network parameters of fortnightly plant–pollinator communities in the restored and the unrestored site. Nestedness values range from 0 to 1, with 1 being maximum nestedness.

Site	Month	Fortnight	Number of plant species	Number of animal species	Ratio animal to plant species	Connectance	Mean degree plants	Maximum degree plants	Mean degree animals	Maximum degree animals	Nestedness[1]
Restored	September	1	12	39	3.25	20.30	7.9	14	2.4	10	0.682*
		2	12	36	3.00	21.53	7.8	20	2.6	6	0.778***
	October	3	13	45	3.46	22.22	10.0	19	2.9	10	0.809***
		4	21	46	2.19	13.87	6.4	16	2.9	12	0.816***
	November	5	34	54	1.59	7.84	4.2	17	2.7	16	0.880***
		6	32	45	1.41	6.67	3.0	15	2.1	10	0.886**
	December	7	29	39	1.34	9.55	3.7	15	2.8	20	0.904**
		8	32	28	0.88	8.04	3.1	11	2.6	9	0.856**
	January	9	20	40	2.00	9.75	3.9	13	2.0	9	0.861*
		10	28	25	0.89	7.29	2.8	10	2.0	5	0.808'
	February	11	17	20	1.18	12.65	2.5	10	2.2	5	0.836*
		12	13	26	2.00	17.75	4.6	9	2.3	7	0.68
	March	13	11	15	1.36	14.55	2.2	4	1.6	3	0.494
Unrestored	September	1	8	31	3.88	19.35	6.0	19	1.5	4	0.813*
		2	11	37	3.36	24.32	9.0	16	2.7	8	0.776***
	October	3	14	37	2.64	25.29	9.4	19	3.5	13	0.721***
		4	17	39	2.29	17.19	6.7	14	2.9	12	0.830***
	November	5	18	35	1.94	15.87	5.6	12	2.9	10	0.817***
		6	23	28	1.22	11.65	3.3	13	2.7	13	0.890***
	December	7	24	13	0.54	13.14	1.7	7	3.2	12	0.872**
		8	19	18	0.95	10.82	1.9	9	2.1	7	0.859*
	January	9	7	22	3.14	20.78	4.6	14	1.5	4	0.847*
		10	17	22	1.29	12.03	2.6	8	2.0	7	0.921*
	February	11	16	27	1.69	13.19	3.6	14	2.1	8	0.827**
		12	19	24	1.26	10.09	2.4	7	1.9	5	0.788
	March	13	17	20	1.18	11.76	2.4	8	2.0	6	0.779

[1] $p < 0.1$ ', $p \leq 0.05$ *, $p \leq 0.001$**, $p \leq 0.0001$ ***

Table 2 Best fit models to the degree distribution in seasonal plant–pollinator networks.

Site	*n*	Set	γ	Best fit
Restored	209	Animals	–0.79	Truncated power-law
		Plants	–0.54	Exponential
Unrestored	163	Animals	–0.76	Truncated power-law
		Plants	–0.57	Truncated power-law

Table 3 Best fit models to the degree distribution of fortnightly plant–pollinator networks. We also present the γ exponent of the power-law fit for animal and plant communities separately.

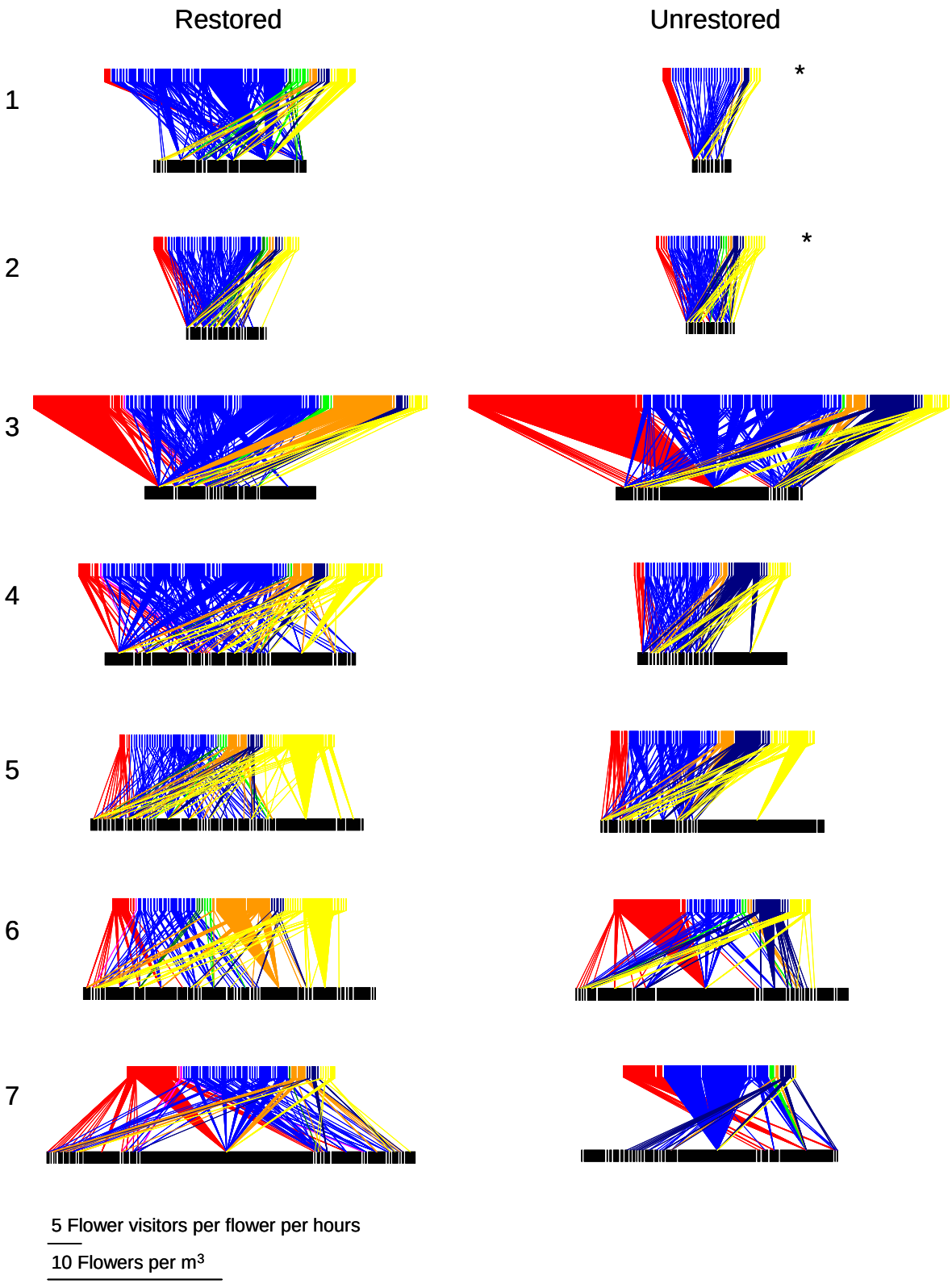
Site	Fortnight	$\gamma_{Animals}$	γ_{Plants}	Best fit models animals[1]	Best fit models plants[1]
Restored	1	1.14	0.36	t	t
	2	0.95	0.63	t	e
	3	0.97	0.52	t	t
	4	1.03	0.76	t	t
	5	1.18	0.62	p	t
	6	1.39	0.74	p	e
	7	1.21	1.16	p	e
	8	1.11	0.69	p	e
	9	1.48	0.68	t	t
	10	1.19	0.78	t	e
	11	1.10	0.76	t	e
	12	1.15	0.45	t	t
	13	1.38	0.62	e	e
Unrestored	1	1.66	0.49	e	t
	2	0.98	0.53	e	e
	3	0.86	0.71	e	e
	4	1.04	1.00	t	e
	5	0.98	0.47	t	t
	6	1.07	0.71	t	e
	7	0.84	0.96	t	e
	8	1.23	0.90	t	t
	9	1.90	0.51	t	e
	10	1.30	0.72	t	t
	11	1.31	0.67	e	e
	12	1.30	0.73	t	e
	13	1.32	0.80	e	e

[1] e = exponential, p = power-law, t = truncated power-law

Table 4 Generalised linear mixed-effects models (GLMM) used to analyse patterns between best fitted models of the degree distribution of fortnightly plant–pollinator networks and network parameters. Best fit of exponential, power-law and truncated power-law (binary: 1 = fitted, 0 = not fitted) was tested against site (restored/unrestored), taxa (plants/animals), squared network size and the mean degree (k) of the network. For each distribution model, we computed a separate analysis. (*df* = numerator degrees of freedom, denominator degrees of freedom)

Best fit	Source	*df*	*F*	*p*
Exponential	Intercept	1, 45	0.64	0.428
	Site	1, 1	1.14	0.479
	Taxon	1, 1	6.42	0.239
	Network size^2	1, 45	0.01	0.927
	Degree	1, 45	1.19	0.281
	Degree × Network size^2	1, 45	0.04	0.835
Power-law	Intercept	1, 45	2.36	0.131
	Site	1, 1	0.00	0.996
	Taxon	1, 1	0.00	0.996
	Network size^2	1, 45	0.37	0.546
	Degree	1, 45	0.22	0.638
	Degree × Network size^2	1, 45	8.77	**0.005**
Truncated power-law	Intercept	1, 45	0.00	0.981
	Site	1, 1	0.16	0.760
	Taxon	1, 1	1.90	0.400
	Network size^2	1, 45	1.33	0.256
	Degree	1, 45	0.55	0.464
	Degree × Network size^2	1, 45	1.09	0.303

FIGURES


Restored
Unrestored
1
2
3
4
5
6
7
*
*
5 Flower visitors per flower per hours
10 Flowers per m3

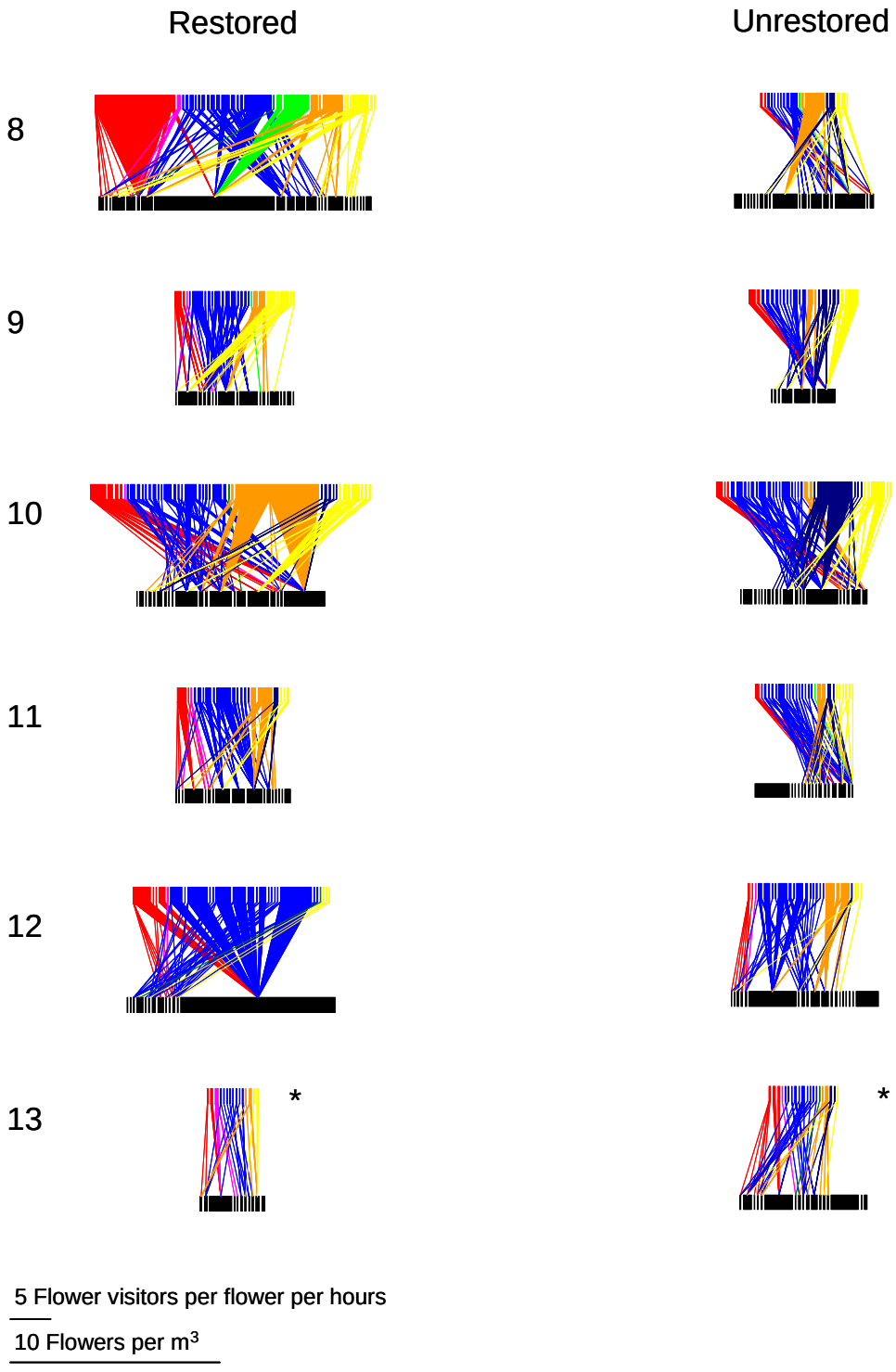


Figure 1 Quantified visitation webs for plant–pollinator communities in the restored and the unrestored site showing temporal and spatial variation of visitation webs. Visitor species are depicted as rectangles at the top and plant species are shown at the bottom (red rectangles depict introduced plant species). The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantified visitation rate between an interacting pair of species.

Webs are drawn to the same scale. * webs are ×2 of the original scale. Red: Hymenoptera, pink: Gekkonidae, light blue: Diptera, dark green: Aves, light green: Hemiptera, orange: Formicidae, dark blue: Coleoptera, and yellow: Lepidoptera.

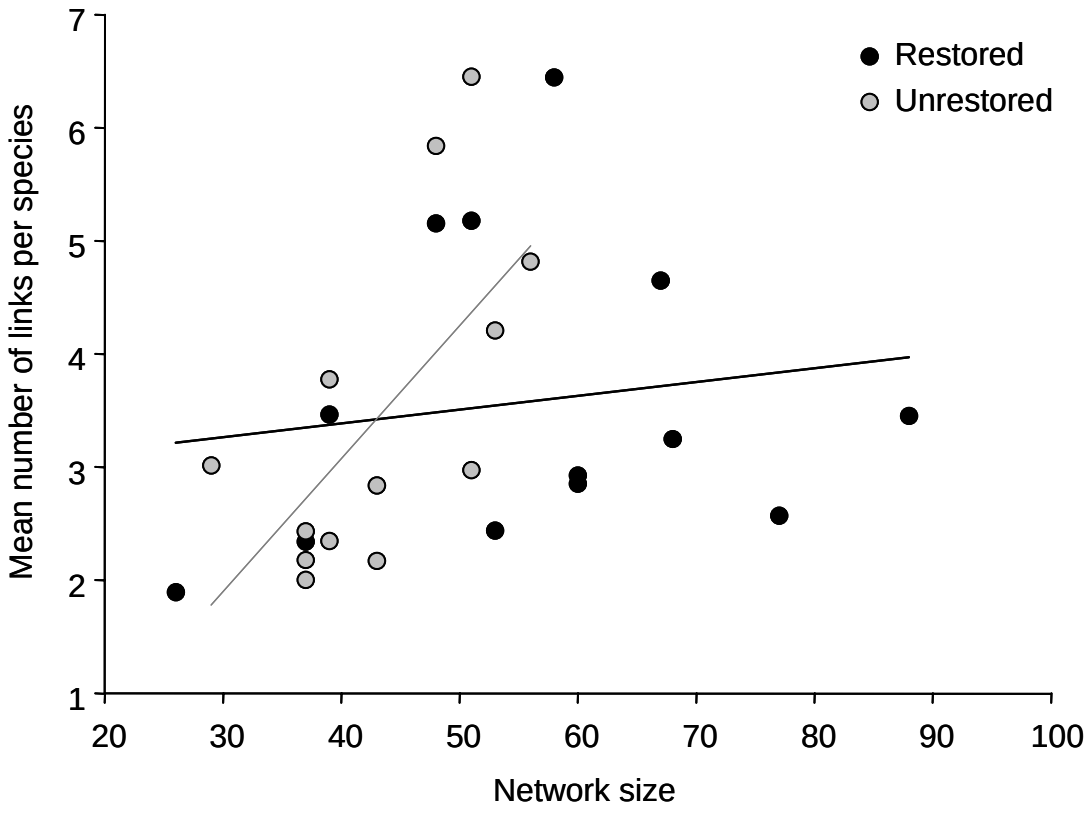


Figure 2 Relationship between the mean number of links per species, k, and network size, *S*, for plant-pollinator networks. Each circle represents one fortnightly network.

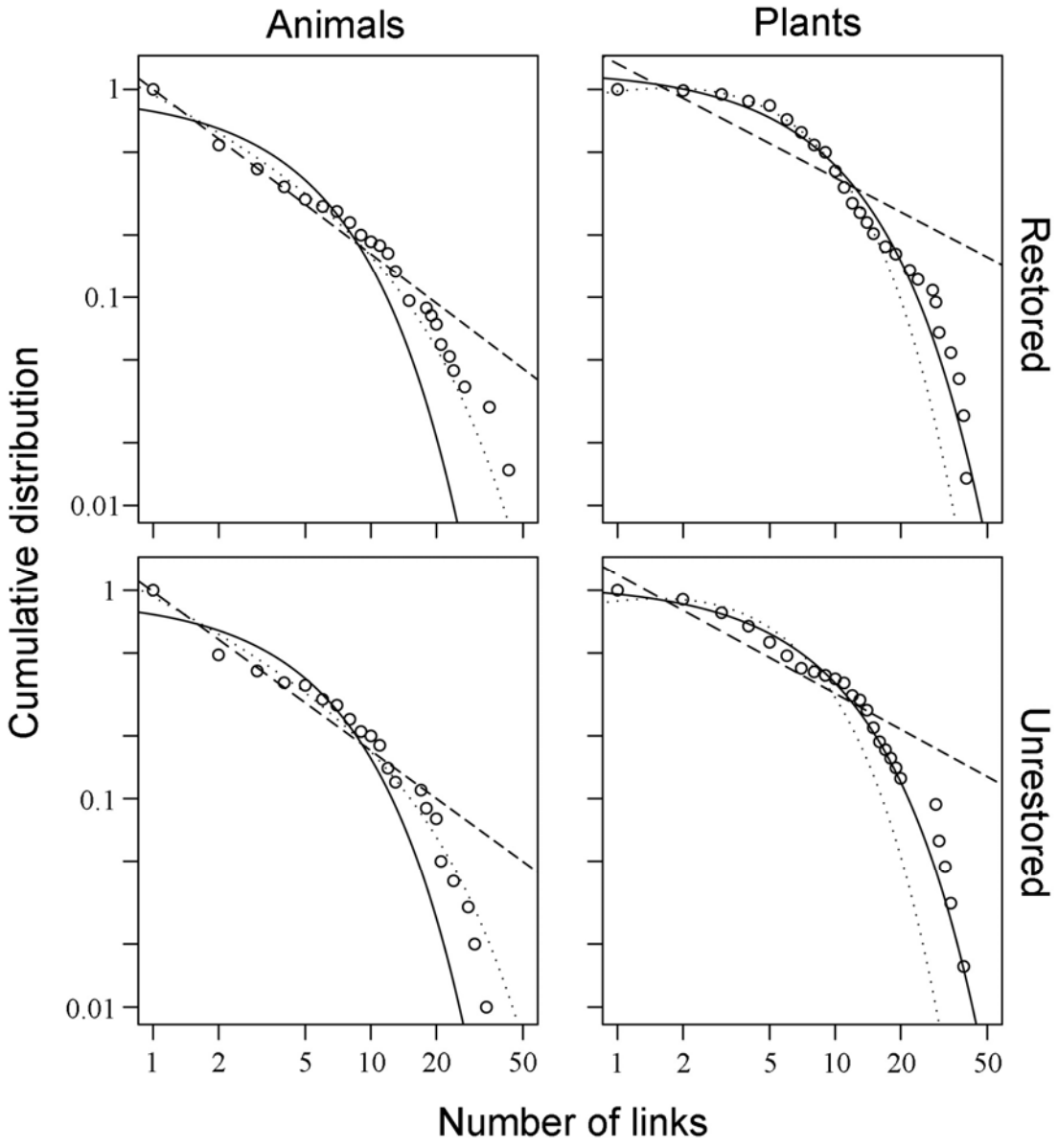


Figure 3 Cumulative distribution of number of links per species (degree) for plant–pollinator networks in the restored and unrestored site. The distributions of links, *P*(k), for animal and plant species are given separately. Panels show the log-log plots of cumulative distribution of species 1, 2, 3 …, k links (circles), exponential fits (solid lines), power-law fits (dashed lines) and truncated power-law fits (dotted lines).

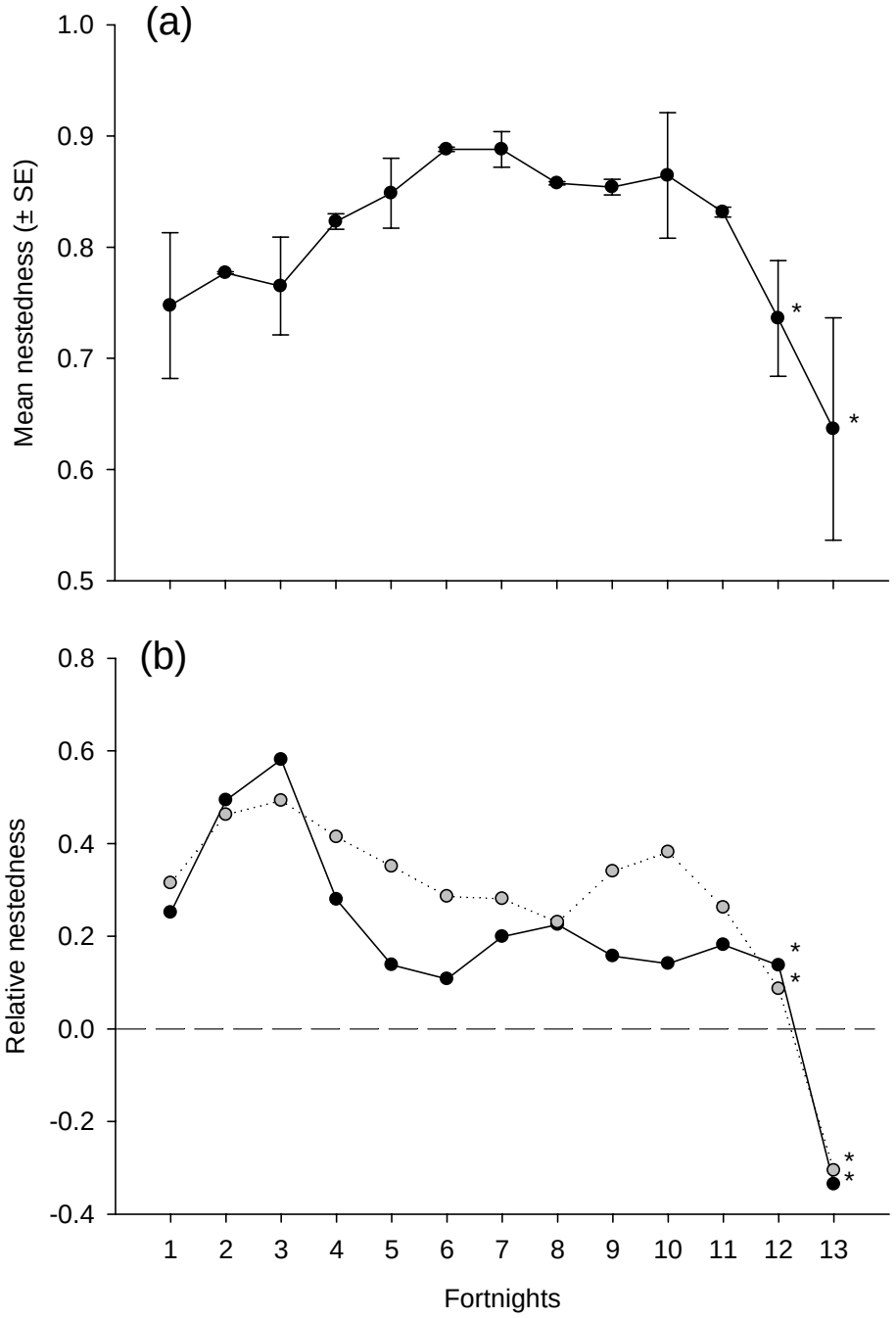


Figure 4 (a) Mean nestedness of fortnightly plant–pollinator networks across site and (b) relative nestedness of networks in (black) the restored and (grey) unrestored site. Relative nestedness indicates the nestedness of a community relative to the average nestedness of the random replicates (based on the number of species and interactions). Networks above the dashed line are more nested than would be expected by chance alone. * indicate not significantly nested networks to the level $p < 0.1$

SUMMARY

This thesis investigates the effects of introduced plant and animal species on native mutualistic interactions, such as pollination and seed dispersal, in Mauritius. Most Mauritian ecosystems are highly degraded by invasive alien plant species, which pose a direct threat to native biodiversity. To conserve endemic plant species and reduce the risk of extinction, conservationists have established a habitat restoration scheme, which focuses on the eradication of introduced plants in fenced plots. However, both the consequences of this restoration for associated animal communities and the role of mutualists in fulfilling their previous ecosystem functions to ensure native plant reproduction are largely unknown.

Chapter 2: we studied the pollination ecology of the endangered endemic cauliflorous tree *Syzygium mamillatum* (Myrtaceae) in a restored forest and an adjacent area heavily degraded by invasive plant species. Flowers of *S. mamillatum* were only visited by generalist bird species. Although gross fruit and seed production of trees in the restored site exceeded those of the unrestored site, fruit and seed set was higher in the degraded forest. This corresponded to the higher bird visitation rate in the unrestored forest. The contrasting avian foraging behaviour may be explained by differences in habitat structure between sites. We conclude that restoration weeding can affect the pollination of *S. mamillatum* in the short-term.

Chapter 3: another critical stage in the plant reproduction cycle, which may be interrupted in degraded ecosystems, is the dispersal of propagules. We studied experimentally the effects of missing propagule dispersal on seed germination and seedling survival of *S. mamillatum*. Our findings provide the first evidence of the significance of the Janzen-Connell model for seedling establishment on an oceanic island. In addition, we demonstrated how ecological analogue species can be used to resurrect extinct seed dispersal interactions.

Chapter 4: we conducted a removal experiment to test whether the presence of the flowering, invasive strawberry guava *Psidium cattleianum* affects the reproductive performance of the neighbouring, endemic plant *Bertiera zaluzania* indirectly via shared pollinators. The introduced honey bee *Apis mellifera* was the most abundant pollinator of *B. zaluzania*. However, we recorded similar visitation rates, fruit set and seed set for *B. zaluzania* plants which were surrounded by *P. cattleianum* flowers and for those where *P. cattleianum* flowers had been removed. The absence of detectable indirect effects indicates

minimal indirect competition for pollination between the introduced strawberry guava and *B. zaluzania*.

Chapter 5: we documented a strong negative effect of the introduced coffee pest *Prophantis smaragdina* on the reproductive success of the endangered Mauritian endemic plant *Bertiera zaluzania*. Most coffee agro-environmental studies focus on the benefits that coffee plants can derive from nearby natural habitats, and neglect to investigate the potential detrimental effects of coffee pest species invading these natural habitats. We present a new perspective to the ongoing scientific debate about coffee and the maintenance of biodiversity in the tropics.

Chapter 6: we used fully quantified flower visitation webs to investigate three main objectives; 1) to compare plant–pollinator community structure of restored and unrestored sites; 2) to identify keystone species of the webs and 3) to determine the effect of introduced species on community structure. Community structure was more complex in the restored than the unrestored site. Visitation webs from both sites were dominated by a few super-abundant, disproportionately-well connected plant and pollinator species, and many rare and specialised species. The dominance of these super-abundant, super-generalist keystone species may be critical, irrespective of their introduced/native status, for ecosystem stability and to ensure reproductive success of a wide range of native plant species. The low visitation rate of introduced plant species suggested a low level of indirect competition for pollination with native plant species. However, the infiltration of the local pollinator community by introduced flower visitors suggested strong competition between native and introduced pollinators for floral resources, which may have resulted in the displacement of native pollinators and consequently the disruption of co-evolved plant–pollinator interactions. For habitat restoration to be successful in the long-term, practitioners should maintain structural diversity to support a species-rich and abundant pollinator assemblage which ensures native plant reproduction.

Chapter 7: we compared flower visitation webs for 13 consecutive fortnightly periods from a restored and an unrestored site (see Chapter 6) and the three network properties connectance, degree distribution and nestedness to describe temporal and spatial variation in plant–pollinator systems and their network topologies. The latter has implications for the stability and the resilience of these networks to perturbations. We found large fluctuations in species diversity (i.e. network size), floral and pollinator abundance between fortnights and sites. The three network properties varied considerably among fortnightly networks and sites, implying that network structure and, thus, network stability and complexity, are not static throughout the season. This may have implications for those animal and plant species which

are phenologically constrained to parts of the season when network stability is low, increasing their susceptibility to disturbance. Potential temporal fluctuation in a range of network properties should be taken into account in future network studies.

ZUSAMMENFASSUNG

Die vorliegende Dissertation befasste sich mit den Wechselbeziehungen zwischen in Mauritius eingeführten Tier- und Pflanzenarten und einheimischen, mutualistischen Tier-Pflanze-Interaktionen, unter anderem Mechanismen der Bestäubung und Samenverbreitung. Alle Daten wurden zwischen Januar 2003 und February 2006 im Black River Gorges Nationalpark in Mauritius erhoben.

Eingeführte Pflanzen- und Tierarten haben zu einer signifikanten Dezimierung der einheimischen, zu hohem Grade endemischen Biodiversität auf Mauritius geführt. Dadurch wurden mutualistische und antagonistische Tier-Pflanze-Interaktionen, die für das reibungslose Funktionieren von Ökosystemen entscheidend sind, erheblich beeinträchigt oder sogar unterbrochen. Um das weiterhin hohe Risiko der Artausrottung zu verringern und die endemische Pflanzenvielfalt zu bewahren, haben mauritische Biologen und Naturschützer seit 1969 mehrere kleine Flächen (ca. 0.1–24 ha) renaturiert. In diesen „Conservation Management Areas“ wurden alle eingeführten Pflanzenarten manuell entfernt, so dass die Artzusammensetzung den ursprünglichen Zustand des Lebensraums widerspiegelt. Es ist jedoch ungeklärt, ob eine solche Habitatrenaturierung auch den für die natürliche Fortpflanzung der einheimischen Pflanzen notwendigen Tieren (z. B. Bestäuber, Samenverbreiter) günstige Rahmenbedingungen schafft. Um dieser Frage nachzukommen, kombinierte ich mehrere integrative Ansätze aus der Bestäubungsbiologie und der Analyse von Netzwerken.

Kapitel 1 umfasste eine allgemeine Einleitung über Restaurationsmassnahmen in Mauritius, den Wandel der Bestäubungsbiologie von Studien einzelner Pflanzenarten bis hin zu ganzen Lebensgemeinschaften, und über die Invasion von eingeführten Arten auf Inseln.

Kapitel 2: Wir studierten die Bestäubungsbiologie der gefährdeten, endemischen Pflanzenart *Syzygium mamillatum* (Myrtaceae) in renaturierten und degradierten Flächen. Generalistische Vogelarten waren die einzigen Blütenbesucher von *S. mamillatum*. Obwohl die gesamte Frucht- und Samenproduktion in der renaturierten Fläche über der der degradierten Fläche lag, war der durchschnittliche Frucht- und Samenansatz in der renaturierten Fläche signifikant geringer. Dieses Ergebnis stimmte mit den beobachteten Vogelbesucherraten überein. Die Unterschiede im Blütenbesucherverhalten stehen wahrscheinlich im Zusammenhang mit markanten Stukturunterschiede in beiden Habitaten. Wir stellen fest, dass der durch die Renaturierungsmassnahmen stattfindende Eingriff in die

Habitatstruktur die Bestäubung von *S. mamillatum*, zumindest in kurzer Hinsicht, beeinträchtigen kann.

Kapitel 3: Wir untersuchten mit Hilfe eines Feldexperiments, inwiefern sich das Ausbleiben von Samenverbreitung auf Samenkeimung und das Wachstum von Keimlingen von *S. mamillatum* auswirkt. Unsere Ergebnisses lieferten die ersten wissenschaftlichen Belege eines ausgeprägten Janzen-Connell Musters bei Keimung und Wachstum von Sämlingen auf einer ozeanischen Insel. Darüber hinaus zeigten wir, dass analoge Arten, die in ihrer ökologischen Funktion den ehemaligen, jetzt ausgestorbenen Arten nahestehen, als geeignete Samenverbreiter von *S. mamillatum* in Frage kommen.

Kapitel 4: Um den indirekten Einfluss von invasiven Arten auf die Bestäubung von einheimischen Pflanzen zu untersuchen, führten wir ein Feldexperiment durch, in dem Blüten der invasiven Art *Psidium cattleianum* in einem Radius von 5m um Pflanzen der endemische Art *Bertiera zaluzania* entfernt wurden. Beide Pflanzenarten wurden regelmässig von der auf Mauritius eingeführte Honigbiene *Apis mellifera* besucht. Frucht- und Samenansatz, sowie die Blütenbesucherrate waren vergleichbar zwischen behandelten und unbehandelten *B. zaluzania* Pflanzen. Die Ergebnisse deuteten an, dass *P. cattleianum* keine Konkurrenz um Bestäuber für *B. zaluzania* darstellt, und dass der Fortpflanzungserfolg von *B. zaluzania* nicht indirekt durch die Präsenz des Eindringlings beeinflusst wird.

Kapitel 5: Wir dokumentierten eine starke Verringerung des Fortpflanzungserfolg von *B. zaluzania* durch den eingeführten Kaffee-Schädling *Prophantis smaragdina*. Die meisten landwirtschaftlich-umweltwissenschaftlichen Studien, die sich mit Kaffeeanbau in den Tropen befassen, beschreiben die Vorteile von Kaffeeplantagen in der unmittelbaren Nähe von natürlichen Lebensräumen. Wenig Aufmerksamkeit wird jedoch den Nachteilen einer solchen Anbaustrategie zugestanden, die zum Beispiel in der Verbreitung von Kaffeeschädlingen in die natürlichen Lebensräume bestehen könnte. Wir präsentierten eine neue Perspektive als Beitrag zur laufenden Debatte über Kaffee und den Erhalt von Biodiversität in den Tropen.

Kapitel 6: Wir verwendeten vollständig quantifizierte Besucher-Netze, um 1) die Pflanzen-Bestäuber-Gemeinschaften einer renaturierten und einer degradierten Fläche miteinander zu vergleichen, 2) Schlüsselarten in beiden Besucher-Netzen zu identifizieren, und 3) den Einfluss von eingeführten Pflanzen- und Tierarten auf die einheimische Pflanzen-Bestäuber-Gemeinschaften zu ermitteln. Die Struktur der renaturierten Gemeinschaft war komplexer als die der degradierten Fläche. Besucher-Netze beider Flächen bestanden hauptsächlich aus wenigen extrem abundanten, überproportional gut verbundenen

(generalistischen) Pflanzen- und Tierarten und einer Grosszahl seltener, spezialisierter Arten. Das Vorkommen von abundanten und vielfach verknüpften Schlüsselarten ist entscheidend für die Stabilität des Ökosystems. Ausserdem spielen die tierischen Schlüsselarten eine zuverlässige Rolle in der Bestäubung vieler einheimischer Pflanzenarten. Eingeführte Pflanzenarten verzeichneten eine sehr geringe Besucherrate, was auf eine geringe Konkurrenz zwischen einheimischen und eingeführten Pflanzenarten schliessen ließ. Die Infiltration der lokalen Bestäubergemeinschaft durch eingeführte Invertebraten war jedoch ein deutliches Zeichen für eine ausgeprägte Konkurrenz zwischen einheimischen und eingeführten Bestäubern um Blütenressourcen, welche zu einer anhaltenden Verdrängung der einheimischen Blütenbesucherfauna und einer Unterbrechung der co-evolvierten Pflanze-Bestäuber-Interaktionen führen kann. Der geringe Fruchtansatz vieler einheimischer Pflanzenarten deutete darauf hin, dass solche Prozesse derzeit schon stattfinden. Damit Habitatrenaturierung auf Dauer erfolgreich sein kann, sollte die strukturelle Diversität der renaturierten Gebiete erhalten werden. Dies unterstützt eine hohe Artenvielfalt, die auf lange Sicht die Fortpflanzung der einheimischen Flora sichern kann.

Kapitel 7: Netzwerkparameter enthalten Informationen über die Stabilität und Resistenz von Netzwerken gegenüber abrupten Veränderungen. Wir untersuchten zeitliche und räumliche Schwankungen in drei Netzwerkparametern von 13 aufeinander folgenden 2-Wochen Perioden in renaturierten und degradierten Flächen, und vergleichen diese mit zeitlichen Veränderungen in Besucher-Netzen. Die Besucher-Netze als auch die Netzwerkparameter zeigen relativ grosse Schwankungen über die Blühsaison. Während der Hauptblühphase deuten die Netzwerkparameter auf einen nicht-randomisierten Aufbau der Netzwerke hin, und gegen Ende der Saison erscheint eine zufällige Anordnung von Tier-Pflanze-Interaktionen und deren Bestäubern wahrscheinlich. Diese Ergebnisse beschreiben Auswirkungen auf phänologisch begrenzte Arten, die hauptsächlich auf Zeiten mit geringer Netzwerkstabilität beschränkt sind. Ausserdem sollten zeitliche und räumliche Unterschiede in Netzwerkeigenschaften bei der Planung von zukünftigen Arbeiten über Pflanze-Bestäuber-Interaktionsnetzwerken beachtet werden.

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Networks are a central theme of this thesis, and they are ubiquitous; this research would not have been possible without the support, help and commitment of a large network of people.

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This PhD took place in two locations, the first half in the field in Mauritius and the second half at the Institute of Environmental Sciences (IfU) in Zurich. In Mauritius, this work would not have been possible without the support of the National Parks and Conservation Service (NPCS) with Yousoof Mungroo as the Director, and the Mauritian Wildlife Foundation. In Zurich, I would like to express my gratitude to the IfU with Bernhard Schmid as the Director for creating such a great scientifically professional and at the same time casual and relaxed working atmosphere.

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I am exceedingly grateful to Nancy. Her love, support and belief in me is never ending, as is our shared passion for Mauritius.

APPENDIX I

The native vertebrate frugivorous fauna of Mauritius. We have omitted the following native, extant species that are known to include fruit in their diet: passerines (*Zosterops* spp.), small diurnal geckos (*Phelsuma* spp.) and small skinks (*Gongylomorphus* spp.) – as they are too small to be of any major importance in dispersing *Syzygium mamillatum* fruits/seeds. Common and scientific names and information on distribution and status are from the latest revision in Cheke & Hume (in press).

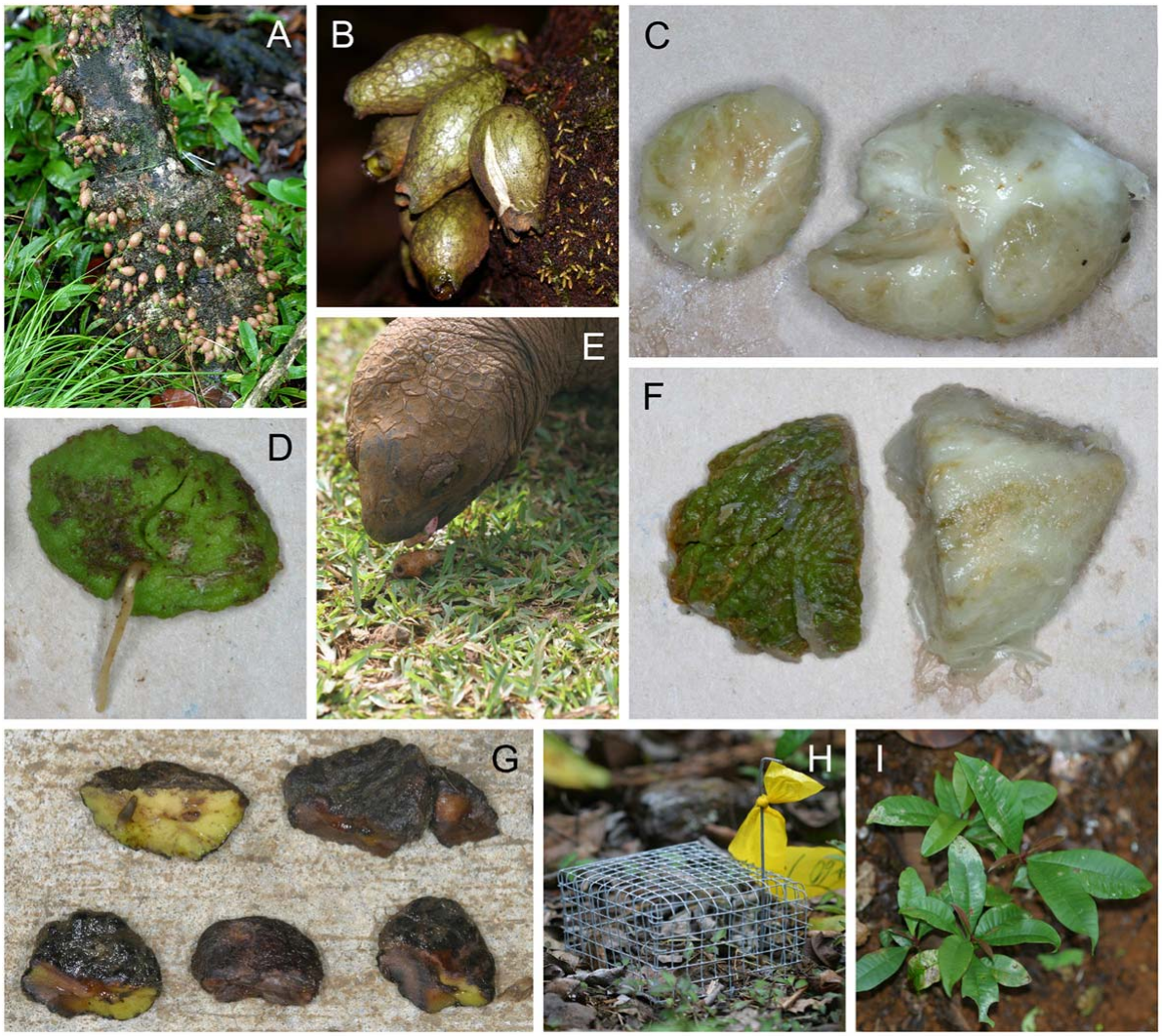
Species	Distribution[1]	Status[2]
Mammals		
Fruit bats: Megachiroptera		
Black-spined Fruitbat *Pteropus niger*	EN M	C
Golden Bat *P. rodricensis*	EN M	EX M
Rougette *P. subniger*	EN M	EX
Birds		
Pigeons and dodos: Columbiformes		
Dodo *Raphus cucullatus*	EN	EX
Dutch Pigeon/Blue Pigeon *Alectroenas nitidissima*	EN	EX
Pink Pigeon *Neosonas mayeri*	EN	CR
Parrots: Psittaciformes		
Raven Parrot *Lophopsittacus mauritianus*	EN	EX
Echo Parakeet *Psittacula eques*	EN M	CR
Thirioux's Grey Parrot *P. bensoni*	EN M	EX
Perching birds: Passeriformes		
Merle *Hypsipetes olivaceus*	EN	END
Reptiles		
Tortoises: Chelonia		
High-backed Tortoise *Cylindraspis triserrata*	EN	EX
Domed Tortoise *C. inepta*	EN	EX
Lizards: Sauria		
Telfair's Skink *Leiolopisma telfairii*	EN	EX RI
Didosaurus *L. mauritiana*	EN	EX
Round Island Day-gecko *Phelsuma guentheri*	EN	EX RI

[1] EN = endemic to Mauritius; EN M = endemic to the Mascarenes.

[2] C = common; END = Endangered; CR = Critically Endangered; EX = extinct; EX M = extinct in Mauritius, extant elsewhere in the Mascarenes; EX RI = extinct on mainland Mauritius, extant on Round Island.

APPENDIX I continued

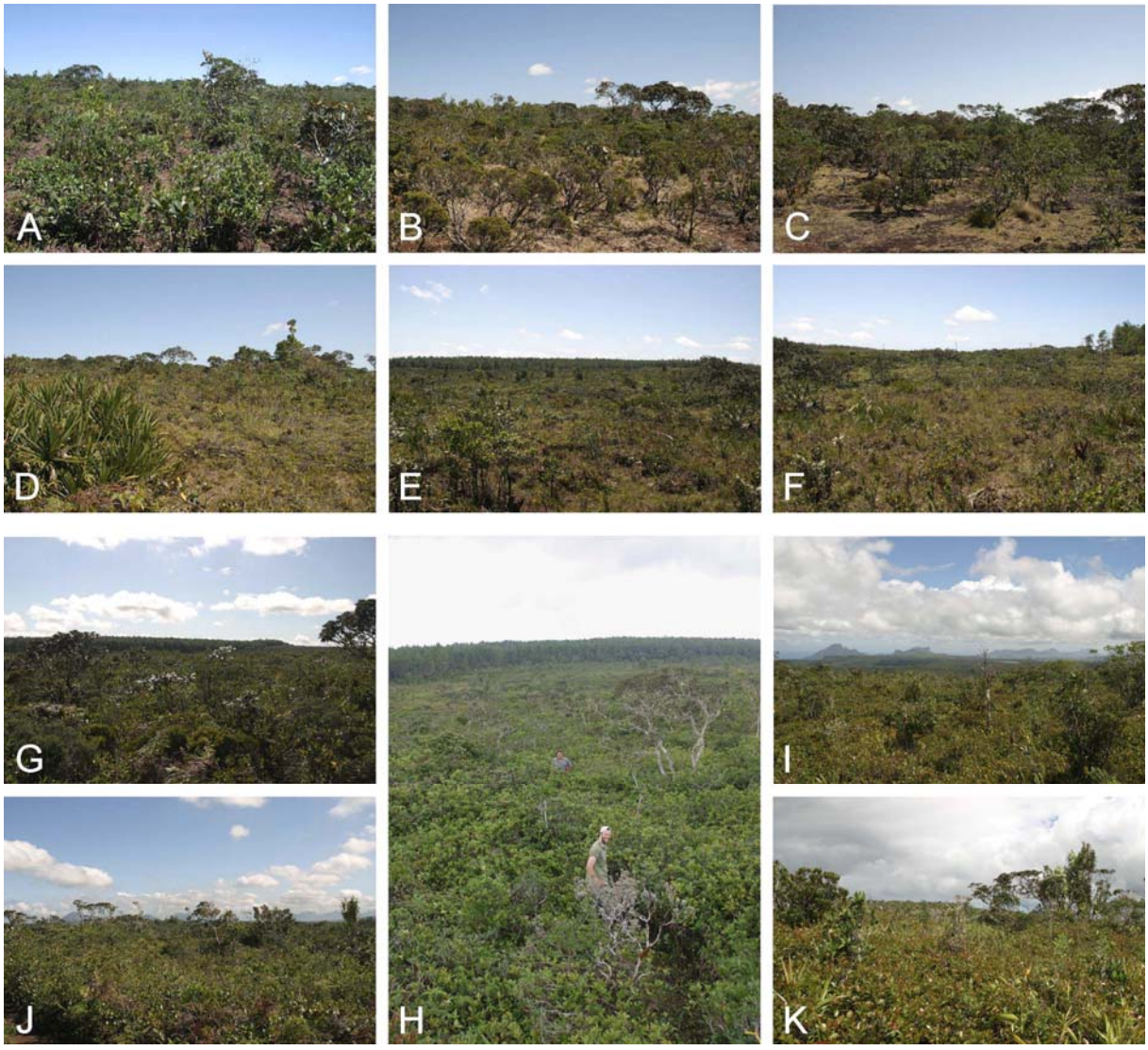
(A) Developing fruits on the lower ~50 cm of a *Syzygium mamillatum* tree. (B) Ripe fruits attached to the trunk. Note the foremost fruit has split open, releasing a fermented smell. (C) A 'ball' of four seeds from one fruit with the pulp removed. (D) Germinating seed. Note the clear line between the two green cotyledons. (E) Giant Aldabra tortoise feeding on *S. mamillatum* fruits. (F) Seeds with and without the slimy, fibrous endocarp. (G) Seed fragments after tortoise gut-passage. Fragments were most often found as whole cotyledons. Note how some cotyledons are still green on the side that faced the other cotyledon, suggesting that they did not break apart until late in the passage. (H) A caged patch of seeds. (I) A patch of seedlings.



APPENDIX II

A – E: Pétrin Conservation Management Area (CMA), initially weeded in 1994, subsequent weeding twice a year; A, B & C: illustrate the typical open structure of the upland heath community at Pétrin; D, E & F: show the species-rich plant community in the marsh area of the CMA.

G – K: Unrestored, heavily degraded area in Pétrin; G, H, J & K: show the dense homogeneous growth of *Psidium cattleianum* (strawberry guava) and the lack of openness compared to the restored habitat; I: illustrates a similarly degraded area at Plaine Champagne (Chapters 3 & 4); H: transect cutting through *P. cattleianum*, note the native plant individuals protruding the invasive thicket.



APPENDIX III

Plant species in the restored and the unrestored site at Pétrin which flowered between September 2003 and March 2004. Presented are species code (corresponding to coding of the visitation webs), origin and status of species, flower type and form (together as flower category), flower colour, mean (± SE) sugar concentration and nectar volume, number of plant individuals (plant abundance), number of attracted pollinator species (linkage), number of visits per flower per hour (visitation rate), quantified visitation rate (visitation rate × floral abundance) and fruit set (data available only for common species, see Chapter 6).

APPENDIX III continued

Site	Plant family	Plant species	Plant code	Origin	Status	Flower category[1]	Flower colour	Sugar concentration (mean % ± SD)	Nectar volume (mean ml ± SE)	Plant individuals	Floral abundance	Linkage	Visitation rate	Quantified visitation rate	Fruit set
restored	Annonaceae	*Xylopia lamarckii*	Xy la	endemic	CR	trap	cream	n.d.	n.d.	22	0.0006	1	0.222	0.001	
unrestored										2	0.0003	0	0	0	
restored	Apocynaceae	*Tabernaemontana persicariaefolia*	Ta per	endemic	EN	salverform	cream	24.0 ± 2.78	1.84 ± 0.23	39	0.053	5	0.290	0.262	
unrestored										6	0.007	3	0.165	0.015	
restored	Araliaceae	*Polyscias mauritiana*	Po ma	endemic	CR	open	brown	n.d.	n.d.	2	0.006	6	0.671	0.020	
restored	Asteraceae	*Faujasiopsis flexuosa ssp erecta*	Fa fl	endemic	VU	open	pink/white	n.d.	n.d.	435	0.025	4	0.061	0.015	1.506
unrestored										164	0.004	9	0.649	0.055	0.866
restored		*Helichrysum proteoides*	He pr	endemic	EN	open	pink/white	n.d.	n.d.	12	0.213	8	0.244	0.394	
unrestored										12	0.297	14	0.438	0.911	
restored		*Psiadia terebinthina*	Psi te	endemic	VU	open	white	n.d.	n.d.	253	1.672	38	0.563	35.549	0.004
unrestored										155	0.484	38	0.568	12.993	0.083
restored	Bignoniaceae	*Colea colei*	Co co	endemic	EN	tubular	purple	22.2 ± 2.58	1.83 ± 0.29	2	0.003	0	0	0	0.111
restored	Rousseaceae	*Roussea simplex*	Ro si	endemic	EN	bell	yellow	11.0 ± 0.42	131.40 ± 27.38	3	0.015	12	1.893	0.280	
restored	Celastraceae	*Pleurostylia leucocarpa*	Pl le	endemic	EN	cup-shaped	green	n.d.	n.d.	3	0.003	8	0.291	0.003	
restored	Chrysobalanaceae	*Grangeria borbonica*	Gr bo	native	VU	open	white	n.d.	n.d.	3	0.009	10	0.220	0.018	
unrestored										7	0.009	14	0.509	0.073	
restored	Clusiaceae	*Calophyllum eputamen var eputamen*	Ca ep	endemic	VU	brush	white	n.d.	n.d.	264	0.008	11	0.521	0.072	
unrestored										32	0.011	4	0.390	0.044	
unrestored		*Harungana madagascariensis*	Ha ma	introduced	–	tubular	white	n.d.	n.d.	8	0.010	3	1.308	0.025	0.249
restored	Dracaenaceae	*Dracaena reflexa var angustifolia*	Dr re	native	LC	tubular	white	12.9 ± 0.61	1.31 ± 0.18	28	0.035	13	0.526	0.104	0.150
unrestored										3	0.003	13	0.625	0.004	
restored	Ebenaceae	*Diospyros revaughanii*	Di re	endemic	VU	cup-shaped	white	25.3 ± 1.96	1.57 ± 0.46	29	0.005	9	1.256	0.140	
unrestored										3	0.001	3	0.698	0.003	
restored	Ericaceae	*Agauria salicifolia*	Ag sa	native	LC	tubular	pink/white	12.6 ± 0.59	0.9 ± 0.2	8	0.020	7	0.170	0.052	0.059
restored	Erythroxylaceae	*Erythroxylum macrocarpum*	Er ma	endemic	VU	cup-shaped	cream	12.5 ± 0.29	10.0 ± 1.35	103	0.036	27	0.622	0.540	0.016
unrestored										35	0.022	29	1.206	0.531	0.079
restored	Euphorbiaceae	*Antidesma madagascariense*	An ma	native	LC	open	red	n.d.	n.d.	7	0.013	13	0.278	0.089	
unrestored										2	0.075	5	0.222	0.276	
restored		*Claoxylon linostachys ssp brachyphyllum*	Cl li	endemic	CR	brush	cream	n.d.	n.d.	11	0.167	18	0.138	0.867	0.023
unrestored										1	0.013	4	0.140	0.007	
restored		*Cordemoya integrifolia*	Co in	native	LC	brush	cream	n.d.	n.d.	46	0.054	4	0.115	0.138	
unrestored										8	0.009	3	0.103	0.018	
restored		*Croton fothergillifolius*	Cr fo	endemic	CR	brush	white	n.d.	n.d.	77	0.358	29	0.349	2.943	0.027
unrestored										46	0.049	28	0.995	1.068	0.006
unrestored		*Croton grangeroides*	Cr gr	endemic	EN	brush	white	n.d.	n.d.	57	0.026	12	0.303	0.248	
unrestored		*Homalanthus populifolius*	Ho po	introduced	–	open	cream	n.d.	n.d.	67	0.035	18	1.131	0.938	0.840
restored		*Phyllanthus phillyreifolius var telfairianus*	Ph ph	endemic	VU	open	red	n.d.	n.d.	22	0.593	7	0.168	2.500	0.021
unrestored										7	0.045	10	0.207	0.203	
restored		*Stillingia lineata ssp lineata*	St li	native	LC	open	yellow	n.d.	n.d.	283	0.112	36	3.098	15.863	0.021
unrestored										234	0.059	33	4.797	11.530	0.014

APPENDIX III continued

Site	Plant family	Plant species	Plant code	Origin	Status	Flower category[1]	Flower colour	Sugar concentration (mean % ± SD)	Nectar volume (mean ml ± SE)	Plant individuals	Floral abundance	Linkage	Visitation rate	Quantified visitation rate	Fruit set
restored	Flacourtiaceae	*Aphloia theiformis*	Ap th	native	LC	brush	white	6.4 ± 0.36	2.6 ± 0.29	1586	0.940	39	1.429	53.086	0.053
unrestored										877	0.279	28	0.799	8.740	0.096
restored		*Casearia coriacea*	Ca co	native	VU	cup-shaped	cream	19.0 ± 1.86	1.7 ± 0.18	292	0.040	2	0.675	0.237	
unrestored										174	0.002	4	0.597	0.005	
restored		*Erythrospermum monticolum var monticolum*	Er mo	endemic	VU	open	white	n.d.	n.d.	20	0.023	9	0.117	0.032	
unrestored										1	0.002	0	0	0	
restored	Flagellariaceae	*Flagellaria indica*	Fl in	native	LC	open	white	n.d.	n.d.	6	0.082	8	0.015	0.018	
unrestored										8	0.030	2	0.112	0.020	0.009
restored	Lauraceae	*Ocotea laevigata*	Oc la	endemic	EN	cup-shaped	cream	n.d.	n.d.	74	0.051	5	0.106	0.058	
restored	Loganiaceae	*Geniostoma borbonicum*	Ge bo	endemic	VU	cup-shaped	white	n.d.	n.d.	24	0.077	23	1.226	1.023	0.011
restored	Loranthaceae	*Bakerella hoyifolia ssp bojeri*	Ba ho	native	EN	salverform	pink/white	13.1 ± 0.84	10.1 ± 2.09	2	0.001	3	0.491	0.002	
restored	Malvaceae	*Trochetia blackburniana*	Tr bl	endemic	EN	bell	red	23.0 ± 1.14	53.2 ± 10.3	89	0.004	1	0.077	0.001	0.933
unrestored										19	0.001	2	0.893	0.004	
unrestored	Melastomataceae	*Clidemia hirta*	Cl hi	introduced	–	cup-shaped	white	n.d.	n.d.	3	0.001	0	0	0	
restored		*Memecylon ovatifolium*	Me ov	endemic	VU	cup-shaped	white	n.d.	n.d.	11	0.015	8	0.183	0.035	
unrestored		*Ossaea marginata*	Os ma	introduced	–	cup-shaped	cream	n.d.	n.d.	223	0.176	0	0	0	0.122
restored		*Tristhema mauritiana*	Tr ma	native	LC	cup-shaped	pink	n.d.	n.d.	4	0.000	1	0.500	0.002	2.500
unrestored										12	0.001	2	0.300	0.002	
restored		*Warneckea trinervis*	Wa tr	endemic	VU	cup-shaped	white	n.d.	n.d.	48	0.205	8	0.270	0.479	0.038
unrestored										27	0.024	2	0.030	0.010	0.012
restored	Meliaceae	*Turraea rigida*	Tu ri	endemic	CR	salverform	pink/white	14.5 ± 0.63	3.1 ± 0.46	11	0.020	4	0.134	0.003	
unrestored										5	0.001	1	0.101	0.057	
restored	Monimiaceae	*Tambourissa peltata*	Ta pe	endemic	EN	cup-shaped	pink	n.d.	n.d.	32	0.002	4	0.857	0.004	
unrestored	Myrsinaceae	*Ardisia crenate*	Ar cr	introduced	–	cup-shaped	white	n.d.	n.d.	36	0.005	0	0	0	1.750
restored		*Badula insularis*	Ba in	endemic	EN	cup-shaped	white	n.d.	n.d.	2	0.020	9	0.372	0.030	0.014
unrestored										2	0.003	2	0.439	0.003	
restored		*Badula platiphylla*	Ba pl	endemic	CR	cup-shaped	pink/white	n.d.	n.d.	10	0.006	6	0.304	0.010	
unrestored										7	0.004	5	0.493	0.014	
restored		*Embelia angustifolia*	Em an	native	EN	cup-shaped	cream	n.d.	n.d.	18	0.055	5	0.431	0.149	0.053
unrestored										3	0.003	6	0.107	0.001	
restored	Myrtaceae	*Eugenia orbiculata*	Eu or	endemic	VU	brush	white	n.d.	n.d.	7	0.001	4	0.824	0.007	
unrestored										30	0.001	1	0.125	0.001	
restored		*Monimiastrum globosum*	Mo gl	endemic	VU	brush	white	n.d.	n.d.	15	0.001	8	0.647	0.003	
unrestored		*Psidium cattleianum*	Ps ca	introduced	–	brush	white	n.d.	n.d.	49626	0.264	11	0.622	4.017	0.167
restored		*Syzygium commersonii*	Sy com	endemic	VU	brush	pink	7.3 ± 0.57	20.4 ± 8.5	4	0.001	2	0.219	0.002	
unrestored										2	0.002	3	0.318	0.003	
restored		*Syzygium coriaceum*	Sy cor	endemic	VU	brush	pink	12.2 ± 0.33	0.4 ± 0.11	475	0.170	18	0.679	2.129	
unrestored										345	0.119	10	0.368	0.746	0.002
restored	Myrtaceae	*Syzygium glomeratum*	Sy gl	endemic	VU	brush	pink	12.3 ± 3.18	0.3 ± 0.11	135	0.003	9	0.602	0.010	
unrestored										113	0.010	3	0.156	0.005	

APPENDIX III continued

Site	Plant family	Plant species	Plant code	Origin	Status	Flower category[1]	Flower colour	Sugar concentration (mean % ± SD)	Nectar volume (mean ml ± SE)	Plant individuals	Floral abundance	Linkage	Visitation rate	Quantified visitation rate	Fruit set
restored		*Syzygium mauritianum*	Sy ma	endemic	EN	brush	pink	4.4 ± 0.48	24.2 ± 14.15	12	0.001	2	0.116	0.0005	
restored		*Syzygium petrinense*	Sy pe	endemic	EN	brush	white	9.2 ± 0.72	2.9 ± 0.45	113	0.052	6	0.384	0.371	0.078
unrestored										10	0.007	8	0.241	0.020	
restored		*Syzygium venosum*	Sy ve	endemic	EN	brush	pink	8.9 ± 0.71	5.6 ± 1.17	9	0.001	5	1.784	0.008	
restored	Ochnaceae	*Ochna mauritiana*	Oc ma	endemic	VU	open	white	n.d.	n.d.	150	0.161	5	0.059	0.188	0.090
unrestored										166	0.139	16	0.951	1.567	0.135
restored	Oleaceae	*Olea lancea*	Ol la	native	LC	cup-shaped	white	n.d.	n.d.	541	0.071	9	0.118	0.137	
unrestored										570	0.073	5	0.359	0.456	0.001
restored	Pandanaceae	*Pandanus barklyi var barklyi*	Pa ba	endemic	EN	open	cream	n.d.	n.d.	12	0.006	5	14.800	0.732	0.053
restored		*Pandanus rigidifolius*	Pa ri	endemic	CR	open	cream	n.d.	n.d.	9	0.001	3	0.462	0.001	
restored		*Pandanus wiehii*	Pa wi	endemic	EN	open	cream	n.d.	n.d.	21	0.028	3	0.600	0.181	
restored	Pittosporaceae	*Pittosporum senacia*	Pi se	native	LC	cup-shaped	cream	15.6 ± 1.44	2.3 ± 0.27	52	0.001	14	0.868	0.010	
unrestored										5	0.002	0	0	0	
unrestored	Rosaceae	*Rubus alcefolius*	Ru al	introduced	–	cup-shaped	white	13.7 ± 0.31	30.3 ± 3.05	68	0.007	4	0.813	0.030	
restored	Rubiaceae	*Antirhea borbonica*	An bo	native	LC	salverform	cream	n.d.	n.d.	1651	0.723	10	0.157	4.592	0.758
unrestored										1157	0.952	10	0.116	3.079	0.368
restored		*Bertiera zaluzania*	Be za	endemic	VU	salverform	cream	19.5 ± 1.05	2.4 ± 0.54	33	0.034	11	0.430	0.197	
unrestored										5	0.008	12	1.467	0.154	
restored		*Chassalia coriacea var coriacea*	Ch co	endemic	EN	salverform	pink	19.8 ± 1.26	0.7 ± 0.1	118	0.113	10	0.228	0.321	0.485
unrestored										20	0.026	7	0.341	0.098	0.545
restored		*Chassalia petrinensis*	Ch pe	endemic	CR	salverform	cream	n.d.	n.d.	2	0.002	4	0.667	0.003	
restored		*Coffea macrocarpa*	Co mac	endemic	VU	cup-shaped	cream	n.d.	n.d.	34	0.018	12	0.597	0.069	0.032
unrestored										21	0.019	4	0.184	0.020	
restored		*Coffea mauritiana*	Co mau	native	VU	cup-shaped	cream	n.d.	n.d.	3	0.006	14	1.088	0.081	
unrestored										6	0.007	1	0.036	0.002	
restored		*Gaertnera petrinensis*	Ga pe	endemic	EN	salverform	white	24.2 ± 1.09	1.1 ± 0.21	102	0.055	7	0.188	0.092	
restored		*Gaertnera psychotrioides/edentata*[2]	Ga ps	endemic	EN	salverform	white	22.1 ± 1.06	1.0 ± 0.06	732	0.173	16	0.480	1.975	
unrestored										196	0.107	17	0.455	1.278	0.011
restored		*Gaertnera rotundifolia*	Ga ro	endemic	CR	salverform	white	18.2 ± 0.55	1.6 ± 0.24	91	0.037	6	0.188	0.184	
unrestored										16	0.020	1	0.048	0.003	
unrestored		*Myonima violacea var ovata*	My vi	endemic	VU	salverform	cream	n.d.	n.d.	23	0.119	13	0.574	1.002	
unrestored		*Psathura terniflora*	Ps te	endemic	VU	salverform	cream	14.5 ± 11.5	14.6 ± 2.05	5	0.001	2	4.000	0.009	
restored		*Pyrostria fasciculata*	Py fa	endemic	EN	salverform	pink/white	16.2 ± 6.17	0.4 ± 0.09	24	0.004	5	0.853	0.034	
restored	Rutaceae	*Euodia chapelieri var chapelieri*	Eu ch	native	EN	cup-shaped	white	n.d.	n.d.	6	0.110	8	0.060	0.183	
restored	Rutaceae	*Euodia obtusifolia ssp gigas var brachypoda*	Eu ob br	endemic	CR	cup-shaped	white	n.d.	n.d.	10	0.001	4	0.048	0.001	
restored		*Euodia obtusifolia ssp gigas var gigas*	Eu ob gi	native	CR	cup-shaped	white	n.d.	n.d.	2	0.041	6	0.185	0.062	
unrestored										1	0.000	1	0.308	0.001	
restored		*Toddalia asiatica*	To as	native	LC	open	cream	n.d.	n.d.	4	0.022	28	0.747	0.260	
unrestored										2	0.008	15	1.678	0.117	
restored	Sapindaceae	*Dodonaea viscosa*	Do vi	native	LC	open	red	n.d.	n.d.	18	0.193	2	0.025	0.137	1.521

APPENDIX III continued

Site	Plant family	Plant species	Plant code	Origin	Status	Flower category[1]	Flower colour	Sugar concentration (mean % ± SD)	Nectar volume (mean ml ± SE)	Plant individuals	Floral abundance	Linkage	Visitation rate	Quantified visitation rate	Fruit set
unrestored	Sapindaceae	*Dodonaea viscosa*	Do vi	native	LC	open	red	n.d.	n.d.	50	0.062	19	0.169	0.361	0.693
restored		*Doratoxylon apetalum var apetalum*	Do ap ap	native	VU	open	pink/white	n.d.	n.d.	230	0.010	4	0.688	0.028	
unrestored		*Doratoxylon apetalum var diphyllum*	Do ap di	native	VU	open	cream	n.d.	n.d.	7	0.005	2	1.000	0.005	
restored		*Molinaea alternifolia*	Mo al	native	VU	open	white	36.4 ± 15.35	0.9 ± 0.29	305	0.073	28	1.487	1.378	0.091
unrestored										184	0.083	19	1.238	1.059	
unrestored		*Molinaea macrantha*	Mo ma	endemic	VU	cup-shaped	pink/white	46.6 ± 1.28	2.1 ± 0.31	3	0.005	3	0.431	0.037	
restored	Sapotaceae	*Labourdonnaisia calophylloides*	La ca	native	VU	bell	white	12.9 ± 0.52	9.9 ± 1.56	307	0.131	6	0.398	0.878	0.013
unrestored										196	0.081	5	0.378	0.615	0.036
restored		*Mimusops erythroxylon*	Mi er	endemic	VU	cup-shaped	brown	n.d.	n.d.	173	0.029	10	0.495	0.200	
restored		*Sideroxylon cinereum*	Si ci	endemic	VU	cup-shaped	red	n.d.	n.d.	265	0.020	21	1.377	0.263	0.629
unrestored										360	0.567	31	1.005	10.609	0.002
restored		*Sideroxylon puberulum*	Si pu	endemic	VU	cup-shaped	red	11.5 ± 0.75	1.2 ± 0.38	594	0.041	33	0.351	0.294	0.343
unrestored										457	0.723	13	0.914	6.455	0.016
restored	Smilacaceae	*Smilax anceps*	Sm an	native	LC	brush	cream	n.d.	n.d.	36	0.004	4	0.053	0.001	0.333
unrestored										26	0.010	1	0.014	0.0003	
unrestored	Thymelaeaceae	*Wikstroemia indica*	Wi in	introduced	–	salverform	yellow	n.d.	n.d.	2027	0.346	1	0.041	0.223	0.086
restored	Xyridaceae	*Xyris sp*	Xy sp	native	–	cup-shaped	yellow	n.d.	n.d.	22	0.018	2	0.063	0.006	

[1] after Endress 1994 and Heywood 1993

[2] *G. psychotrioides* and *G. edentata* are indistinguishable in the field

APPENDIX IV

Pollinator species observed on flowering plant species between September 2003 and March 2004 in the restored and the unrestored site at Pétrin. Presented are species code (corresponding to coding of the visitation webs), the species origin, the total number of visits, the mean number of probed flowers per visit (± SE), the number of visited plant species (linkage) and the specialisation index of the pollinator (s_i) and the mean level of specialisation of visited plant species (p_i; for more explanation see Chapter 6).

APPENDIX IV continued

Site	Animal order	Animal family	Animal species	Animal code	Origin	Number of visits	Mean ± SE probed flowers per visit	Linkage	s_i	p_i
restored	Coleoptera	Cerambycidae	*Cerambycidae* sp 1	22	unknown	2	1.50 ± 0.50	2		
unrestored						4	2.25 ± 0.25	2		
unrestored			*Cerambycidae* sp 2	23	unknown	1	1.00	1		
restored			*Cerambycidae* sp 3	24	unknown	2	1.00 ± 0.00	2		
unrestored						1	2.00	1		
restored			*Mauritiborium undulatus*	87	endemic	4	2.25 ± 0.25	3		
unrestored						14	1.71 ± 0.30	6	5.25	5.81
restored		Chrysomelidae	*Chaetocnema* sp	26	introduced	94	1.64 ± 0.12	15	5.69	6.18
unrestored						702	1.73 ± 0.05	34	7.30	5.08
unrestored			*Cryptocephalinae* sp	39	unknown	1	1.00	1		
restored			*Eumolpinae* sp 1	52	unknown	1	1.00	1		
unrestored			*Eumolpinae* sp 2	53	unknown	1	2.00	1		
unrestored			*Eumolpinae* sp 3	54	unknown	5	1.80 ± 0.20	2		
restored		Coccinellidae	*Hyperaspis hottentota*	71	unknown	1	2.00	1		
restored		Cucujidae	*Ahasverus advena*	7	introduced	8	1.50 ± 0.19	5		
unrestored						14	2.21 ± 0.32	5	4.13	5.78
unrestored		Curculionidae	*Cratopus psittacus*	37	unknown	1	7.00	1		
restored		Melyridae	*Dasytinae* sp	40	unknown	1	1.00	1		
unrestored						1	3.00	1		
restored			*Pelecophora intemipta*	113	unknown	9	2.33 ± 0.65	4		
unrestored						5	2.00 ± 0.32	3		
restored		Mordellidae	*Mordellidae* sp 1	92	unknown	6	1.17 ± 0.17	2		
unrestored						1	3.00	1		
restored			*Mordellidae* sp 2	93	unknown	1	1.00	1		
unrestored						1	3.00	1		
unrestored			*Mordellidae* sp 3	94	unknown	1	1.00	1		
unrestored		Nitidulidae	*Nitidulidae* sp	100	unknown	1	1.00	1		
restored		Scirtidae	*Scirtidae* sp 1	131	unknown	1	1.00	1		
unrestored						1	3.00	1		
restored			*Scirtidae* sp 2	132	unknown	1	1.00	1		
unrestored						1	1.00	1		
restored	Diptera	Acalyptrate	*Acalyptrate* sp	1	unknown	3	2.00 ± 0.58	1		
restored		Agromyzidae	*Melanagromyza sojae*	88	introduced	5	4.00 ± 1.05	4		
unrestored						1	2.00	1		
restored		Anthomyiidae	*Anthomyia faciata*	12	native	1	2.00	1		
restored		Bombyliidae	*Villa unifasciata*	156	native	68	3.06 ± 0.24	19	6.53	5.61
unrestored						51	1.96 ± 0.16	17	6.97	5.51
restored		Calliphoridae	*Chrysomya megacephala*	31	native	129	5.16 ± 0.50	27	7.68	5.82
unrestored						67	5.31 ± 0.78	17	6.44	5.49
restored			*Stomorhina lunata*	142	introduced	444	4.81 ± 0.25	35	6.61	5.96

APPENDIX IV continued

Site	Animal order	Animal family	Animal species	Animal code	Origin	Number of visits	Mean ± SE probed flowers per visit	Linkage	s_i	p_i
unrestored	Diptera	Calliphoridae	*Stomorhina lunata*	143	introduced	225	5.87 ± 0.39	30	7.19	5.41
restored		Chironomidae	*Chironomidae* sp	30	unknown	1	1.00	1		
restored		Dolichopodidae	*Dolichopodidae* sp	44	unknown	2	1.00 ± 0.00	1		
restored		Drosophilidae	*Drosophila* sp 1	45	unknown	1	1.00	1		
restored			*Drosophila* sp 2	46	unknown	2	1.00 ± 0.00	1		
restored			*Drosophila* sp 3	47	unknown	5	1.6 ± 0.24	2		
restored			*Zaprionus tuberculatus*	157	introduced	3	1.00 ± 0.00	1		
restored		Drosophilidae	*Zaprionus vittiger*	158	introduced	1	1.00	1		
restored		Ephydridae	*Hyadina* sp	68	unknown	2	3.00 ± 1.00	2		
restored			*Psilopa iceryae*	120	introduced	26	2.27 ± 0.36	11	5.84	5.20
restored		Fanniidae	*Fannia pusio*	56	introduced	95	3.41 ± 0.21	11	4.88	6.25
unrestored						121	3.12 ± 0.20	11	4.03	4.83
restored		Lauxaniidae	*Homoneura quadrivittata*	65	endemic	2	1.00 ± 0.00	1		
restored			*Homoneura* sp 1	66	endemic	1	1.00	1		
unrestored						1	6.00	1		
restored			*Homoneura* sp 2	67	endemic	5	2.40 ± 1.17	2		
unrestored						1	3.00	1		
restored			*Lauxania* sp	73	unknown	1	1.00	1		
restored			*Pachycerina crinicornis*	107	endemic	288	3.03 ± 0.14	35	7.10	5.74
unrestored						87	2.91 ± 0.27	21	6.17	5.57
restored			*Sapromyza* sp near *nudiuscula*	127	unknown	9	4.33 ± 1.41	5		
unrestored						4	1.50 ± 0.29	4		
restored		Limoniidae	*Limonia (Dycranomia)* sp	78	unknown	1	1.00	1		
restored			*Limoniidae* sp	79	unknown	1	2.00	1		
unrestored		Muscidae	*Atherigona orientalis*	14	native	1	2.00	1		
restored			*Atherigona* sp	15	unknown	1	3.00	1		
restored			*Graphomya maculata*	62	native	18	2.67 ± 0.89	7	4.81	6.65
unrestored						1	1.00	1		
unrestored			*Hydrotaea fuliginosa*	70	native	2	3.00 ± 0.00	1		
restored			*Limnophora quaterna*	77	introduced	4	1.75 ± 0.25	2		
unrestored						1	1.00	1		
unrestored			*Musca confiscata*	95	native	1	3.00	1		
restored			*Musca domestica*	96	introduced	133	3.35 ± 0.30	23	7.01	6.23
unrestored						132	4.98 ± 0.57	20	6.21	5.53
restored			*Ophyra capensis*	103	introduced	24	3.33 ± 0.48	8	5.19	6.43
unrestored						33	5.67 ± 1.05	8	4.59	5.86
restored			*Orchisia costata*	104	native	2	1.00 ± 0.00	2		
unrestored						2	2.00 ± 1.00	2		
restored			*Orthellia albigena*	106	native	9	4.00 ± 1.21	7		

APPENDIX IV continued

Site	Animal order	Animal family	Animal species	Animal code	Origin	Number of visits	Mean ± SE probed flowers per visit	Linkage	s_i	p_i
restored	Diptera	Muscidae	*Spilogona* sp	140	unknown	1	2.00	1		
restored			*Stomoxys calcitrans*	143	introduced	48	2.10 ± 0.31	13	6.80	6.45
unrestored						38	4.32 ± 0.68	10	6.21	5.27
restored			*Stomoxys niger*	144	introduced	47	1.98 ± 0.32	10	5.01	6.09
unrestored						22	2.50 ± 0.35	7	5.21	5.91
restored		Mycetophilidae	*Lygistorrhina* sp	85	native	43	5.58 ± 0.66	9	4.87	5.54
unrestored						56	3.61 ± 0.55	11	5.30	5.23
restored		Sarcophagidae	*Sarcophaga arno*	128	introduced	9	5.00 ± 1.27	6		
unrestored						9	3.00 ± 1.04	7		
restored		Scatopsidae	*Scatopsidae* sp	130	unknown	1	3.00	1		
unrestored						1	2.00	1		
restored		Sepsidae	*Sepsis lateralis*	136	introduced	10	4.10 ± 1.03	3	3.00	6.00
restored		Simuliidae	*Simulium (Byssodon)* sp 2	137	introduced	1	6.00	1		
unrestored	Diptera	Simuliidae	*Simulium (Byssodon)* sp 2	137	introduced	1	1.00	1		
restored			*Simulium* sp	138	unknown	1	2.00	1		
restored		Syrphidae	*Allograpta nasuta*	8	native	42	3.74 ± 0.62	20	8.01	5.98
unrestored						63	4.48 ± 0.56	20	7.88	5.28
restored			*Allograpta* sp 1	9	unknown	1	3.00	1		
restored			*Allograpta* sp 2	10	unknown	4	3.75 ± 1.80	1		
restored			*Episyrphus* sp near *circularis*	50	native	24	4.38 ± 0.98	13	6.63	5.85
unrestored						22	2.50 ± 0.55	12	6.90	5.68
restored			*Eristalinus flaveolus*	51	native	51	3.35 ± 0.34	18	7.11	6.06
unrestored						27	4.22 ± 0.80	11	6.16	5.25
restored			*Ischiodon aegyptius*	72	introduced	21	3.43 ± 0.69	12	6.97	5.76
unrestored						17	3.88 ± 1.37	7	5.19	5.28
restored			*Melanostoma annulipes*	89	native	72	1.88 ± 0.21	12	5.59	6.19
unrestored						35	1.91 ± 0.20	10	6.18	5.73
restored			*Melanostoma bituberculatum*	90	introduced	14	4.14 ± 0.63	6	5.07	6.35
unrestored						10	4.30 ± 1.05	6		
restored			*Ornidia obesa*	105	introduced	21	2.76 ± 0.56	13	7.61	4.99
unrestored						8	6.00 ± 1.43	8		
restored			*Paragus borbonicus*	112	introduced	75	4.80 ± 0.55	21	6.51	6.10
unrestored						15	4.13 ± 1.44	9		
unrestored			*Syritta bulbus*	146	introduced	4	3.00 ± 0.41	1		
restored			*Syritta nigrofemorata*	147	native	16	3.94 ± 0.76	8	6.51	6.28
unrestored						17	3.94 ± 0.82	8	6.13	5.99
restored			*Syritta* sp near *abyssinica*	148	introduced	10	3.80 ± 0.90	7	7.00	6.28
unrestored						6	3.83 ± 1.08	3		
unrestored		Tachinidae	*Palexorista* sp	109	native	1	2.00	1		

APPENDIX IV continued

Site	Animal order	Animal family	Animal species	Animal code	Origin	Number of visits	Mean ± SE probed flowers per visit	Linkage	s_i	p_i
restored	Diptera	Tachinidae	*Phorinia* sp	118	native	59	3.66 ± 0.29	12	5.68	6.02
unrestored						10	1.80 ± 0.33	5	5.00	5.53
restored			*Siphona* sp	139	unknown	3	1.33 ± 0.33	2		
unrestored						1	4.00	1		
restored			*Thelairodrino* sp	152	unknown	1	3.00	1		
unrestored						1	1.00	1		
restored		Tephritidae	*Bactrocera cucurbitae*	16	introduced	2	1.50 ± 0.5	2		
restored			*Ceratitis roas*	25	introduced	5	2.40 ± 0.40	3		
unrestored						1	1.00	1		
restored			*Dioxyna sororcula*	41	introduced	11	2.73 ± 0.14	5	4.82	6.35
unrestored						25	3.12 ± 0.37	7	4.21	6.20
restored			*Goniurellia or Dectodes* sp	61	unknown	9	3.44 ± 0.75	3		
unrestored						2	2.00 ± 0.00	1		
restored			*Trirhithrum* sp near *nigerrimum*	155	unknown	7	2.14 ± 0.26	3		
restored		Unknown	*Diptera* sp 1	42	unknown	7	3.57 ± 0.61	1		
unrestored			*Diptera* sp 2	43	unknown	1	2.00	1		
unrestored			*Diptera* sp 3	42	unknown	1	2.00	1		
restored	Hemiptera	Cicadellidae	*Acopsis viridicans*	3	native	4	1.75 ± 0.25	3		
restored			*Cicadellidae* sp	32	unknown	1	1.00	1		
unrestored		Cixiidae	*Cixiidae* sp 1	33	unknown	1	3.00	1		
unrestored	Hemiptera	Cixiidae	*Cixiidae* sp 2	34	unknown	1	1.00	1		
restored		Lygaeidae	*Lygaeidae* sp 1	80	unknown	1	2.00	1		
unrestored			*Lygaeidae* sp 2	81	unknown	1	5.00	1		
unrestored			*Lygaeidae* sp 3	82	unknown	1	1.00	1		
restored			*Lygaeidae* sp 4	83	unknown	1	3.00	1		
restored			*Lygaeidae* sp 5	84	unknown	13	2.31 ± 0.50	3	2.92	6.07
unrestored						22	3.09 ± 0.38	1	1.00	7.02
restored		Miridae	*Miridae* sp	91	unknown	5	1.40 ± 0.24	4		
unrestored						1	8.00	1		
restored		Nogodinidae	*Nogodinidae* sp	101	unknown	5	2.00 ± 0.45	1		
restored		Psyllidae	*Psyllidae* sp 1	121	unknown	1	1.00	1		
restored			*Psyllidae* sp 2	122	unknown	1	1.00	1		
unrestored						1	1.00	1		
restored		Ricaniidae	*Tarundia servillei*	149	unknown	5	1.80 ± 0.37	4		
restored		Tettigoniidae	*Conocephalus* sp 1	35	unknown	1	1.00	1		
restored			*Tettigoniidae* sp 1	151	unknown	1	1.00	1		
restored	Hymenoptera	Apidae	*Apis mellifera*	13	introduced	645	6.94 ± 0.27	43	7.02	5.08
unrestored						682	8.80 ± 0.35	28	6.32	3.98
unrestored		Braconidae	*Agathidinae* sp	5	unknown	1	5.00	1		

APPENDIX IV continued

Site	Animal order	Animal family	Animal species	Animal code	Origin	Number of visits	Mean ± SE probed flowers per visit	Linkage	s_i	p_i
unrestored	Hymenoptera	Braconidae	*Agathidinae sp*	5	unknown	3	3.67 ± 0.67	1		
restored			*Cheloninae* sp 2	28	unknown	1	2.00	1		
unrestored			*Cheloninae* sp 3	29	unknown	2	1.00	1		
unrestored			*Cotesia* sp 1	36	unknown	3	1.33 ± 0.33	1		
restored		Calcidoidae	*Calcidoidae* sp 1	18	unknown	1	3.00	1		
unrestored			*Eurytonidae* sp 1	55	unknown	1	3.00	1		
restored		Colletidae	*Paleorhiza* sp 1	108	native	1	3.00	1		
restored		Formicidae	*Brachymyrmex* sp	17	native	228	1.83 ± 0.12	20	6.81	5.07
unrestored						96	1.92 ± 0.10	12	5.95	5.09
restored			*Pheidole megacephala*	116	introduced	16	1.69 ± 0.15	1	1.00	2.70
unrestored						3	2.00 ± 0.00	1		
restored			*Technomyrmex albipes*	150	introduced	456	2.05 ± 0.08	45	7.61	4.62
unrestored						236	2.10 ± 0.08	24	7.07	4.27
restored		Ichneumonidae	*Campopleginae* sp	20	unknown	1	4.00	1		
unrestored						2	2.00 ± 0.00	1		
restored			*Cryptinae* sp	38	unknown	1	1.00	1		
restored		Pteromalidae	*Pteromalidae* sp	123	unknown	3	2.00 ± 0.58	1		
restored		Scoliidae	*Scolia carniflex*	133	introduced	1	3.00	1		
unrestored						1	9.00	1		
restored			*Scolia oryctophaga*	134	introduced	1	11.00	1		
restored		Vesperidae	*Polistes hebraeus*	119	introduced	42	4.71 ± 0.60	13	6.16	4.99
unrestored						34	4.68 ± 0.66	13	6.59	5.43
restored	Lepidoptera	Arctiidae	*Dysauxes florida*	48	endemic	5	1.8 ± 0.37	3		
unrestored						163	6.52 ± 0.52	18	6.01	5.30
restored			*Eilema squalida*	49	native	4	4.75 ± 0.75	2		
restored			*Nyctemera insulare*	102	native	3	1.33 ± 0.33	2		
unrestored						1	7.00	1		
restored		Crambidae	*Nacoleia* sp 1	98	unknown	252	2.37 ± 0.15	24	7.10	3.76
unrestored	Lepidoptera	Crambidae	*Nacoleia* sp 2	99	unknown	78	2.24 ± 0.20	20	6.43	5.43
restored			*Nacoleia* sp 2	99	unknown	15	1.87 ± 0.17	7	5.83	5.99
unrestored						19	1.84 ± 0.37	5	3.79	5.55
restored			*Scopariinae* sp	135	unknown	3	2.00 ± 0.58	2		
unrestored						2	1.00 ± 0.00	2		
restored		Gelechiidae	*Gelechioidea* sp 1	58	unknown	2	2.00 ± 0.00	2		
unrestored						1	4.00	1		
unrestored			*Gelechioidea* sp 2	59	unknown	16	2.00 ± 0.22	5	4.10	5.86
unrestored			*Gelechioidea* sp 3	60	unknown	2	1.50 ± 0.50	2		
restored			*Lecithoceridae* sp 1	74	unknown	6	1.83 ± 0.31	4		
unrestored						3	1.67 ± 0.67	3		

APPENDIX IV continued

Site	Animal order	Animal family	Animal species	Animal code	Origin	Number of visits	Mean ± SE probed flowers per visit	Linkage	s_i	p_i
restored	Lepidoptera	Hesperiidae	*Panara naso*	110	native	31	2.55 ± 0.34	13	5.73	5.03
unrestored						31	3.19 ± 0.33	11	5.24	5.13
restored		Hypsidae	*Aganais borbonica*	4	native	1	2.00	1		
restored		Lycaenidae	*Leptotes pirithous*	76	native	16	3.06 ± 0.64	8	6.31	5.92
unrestored				76	native	14	4.00 ± 0.62	5	4.13	5.50
restored			*Zizeeria knysa*	159	native	1	2.00	1		
restored		Macroglossidae	*Macroglossum milvus*	86	native	6	16.33 ± 5.28	2		
unrestored						2	4.50 ± 2.50	2		
restored		Noctuidae	*Achaea finita*	2	native	1	5.00	1		
restored			*Agrostis atritegulator*	6	unknown	1	6.00	1		
restored			*Condica capensis*	11	native	1	1.00	1		
restored			*Hydrillodes* sp	69	native	8	1.25 ± 0.16	2		
restored			*Mythimna* sp	97	unknown	1	2.00	1		
restored			*Remigia frugalis*	126	unknown	1	2.00	1		
restored			*Sarrothripinae* sp	129	unknown	1	2.00	1		
restored			*Spodoptera littoralis*	141	introduced	1	6.00	1		
restored			*Strictopterinae* sp	145	unknown	1	2.00	1		
unrestored			*Thysanoplusia orichalcea*	153	native	1	3.00	1		
restored			*Trichoplusia indicator*	154	native	4	4.75 ± 1.89	2		
restored		Nymphalidae	*Henotesia narcissus*	63	native	26	2.00 ± 0.21	9	4.26	5.94
unrestored						4	3.50 ± 1.32	2		
restored			*Phalanta phalantha*	115	native	1	6.00	1		
unrestored						1	1.00	1		
restored		Papillionidae	*Papillio manlius*	111	endemic	1	7.00	1		
unrestored		Pieridae	*Calopsilia florella*	19	introduced	1	1.00	1		
restored		Pterophoridae	*Pterophoridae* sp	124	unknown	1	1.00	1		
restored		Sphingidae	*Cephonodes trochilus*	21	native	6	8.17 ± 4.83	4		
restored			*Hippotion eson*	64	native	8	12.13 ± 4.81	3		
unrestored						1	1.00	1		
restored	Passeriformes	Ploceidae	*Foudia madagascariense*	57	introduced	1	106.00	1		
restored		Pycnonotidae	*Pycnonotus jocosus*	125	introduced	1	37.00	1		
restored		Zosteropidae	*Zosterops mauritianus*	160	endemic	31	10.94 ± 3.11	8	5.80	5.60
unrestored						3	4.00 ± 0.58	2		
restored	Squamata	Gekkonidae	*Phelsuma cepediana*	117	endemic	44	6.93 ± 1.29	12	4.45	3.94
unrestored						5	4.60 ± 2.46	3		

APPENDIX V

Number (%) of native, introduced and total flower visitor species within their families. No origin could be assigned to unidentified species.

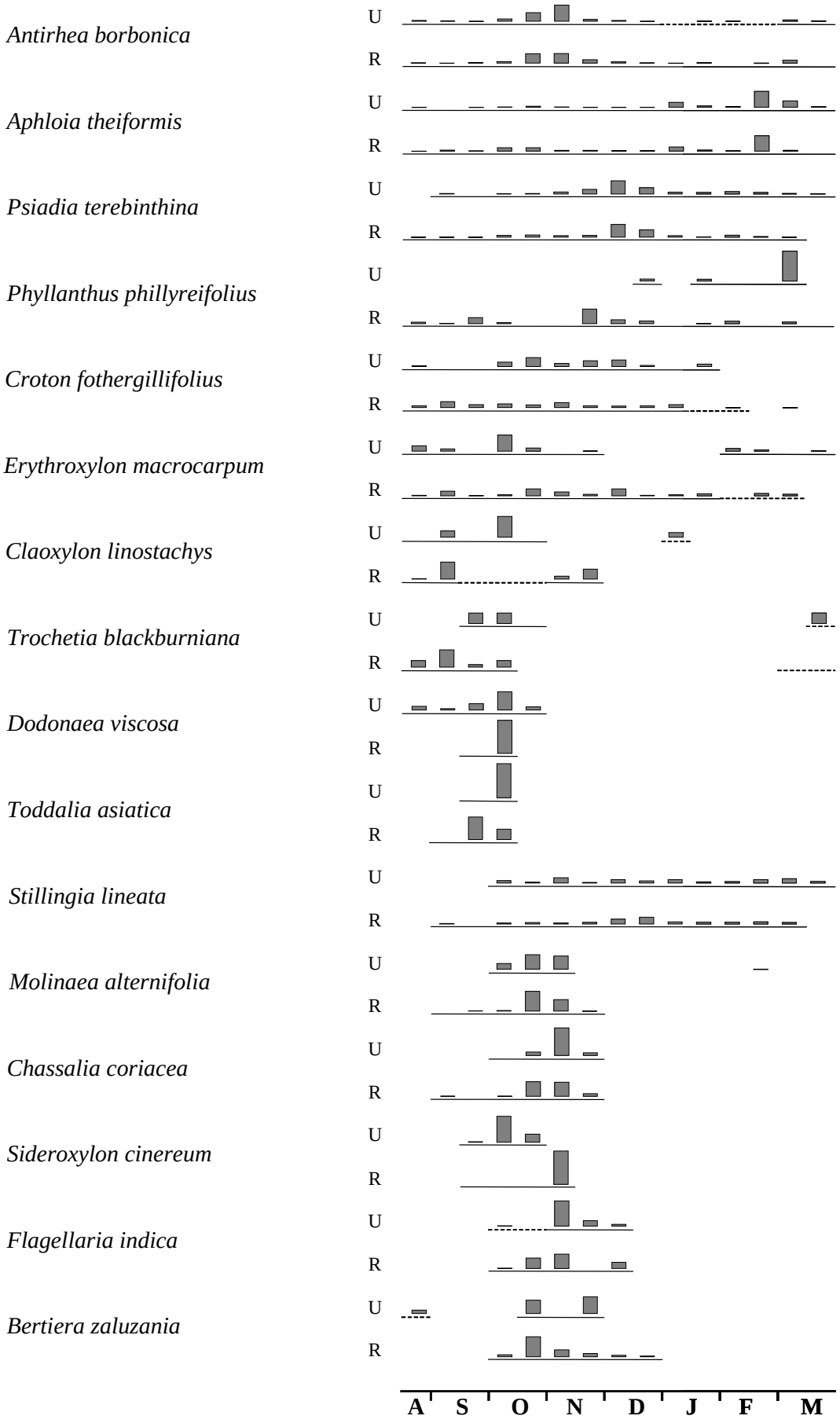
		Total			Restored			Unrestored		
Order	Family	Number of species	Number (%) of native species	Number (%) of introduced species	Number of species	Number (%) of native species	Number (%) of introduced species	Number of species	Number (%) of native species	Number (%) of introduced species
Hemiptera	Cicadellidae	2	1 (50)		2	1 (50)				
	Cixiidae	2						2		
	Lygaeidae	5			3			3		
	Miridae	1			1			1		
	Nogodinidae	1			1					
	Psyllidae	2			1			1		
	Ricaniidae	1			1					
	Tettigoniidae	2			2					
Hymenoptera	Apidae	1		1 (100)	1		1 (100)	1		1 (100)
	Braconidae	5			2			4		
	Calcidoidae	2			1			1		
	Colletidae	1	1 (100)		1	1 (100)				
	Formicidae	3	1 (33)	2 (67)	3	1 (33)	2 (67)	3	1 (33)	2 (67)
	Ichneumonidae	2			2			1		
	Pteromalidae	1			1					
	Scoliidae	2		2 (100)	2		2 (100)	1		1 (100)
	Vesperidae	1		1 (100)	1		1 (100)	1		1 (100)
Lepidoptera	Arctiidae	3	3 (100)		3	3 (100)		2	2 (100)	
	Crambidae	3			3			3		
	Gelechiidae	5			3			4		
	Hesperiidae	1	1 (100)		1	1 (100)		1	1 (100)	
	Hypsidae	1	1 (100)		1	1 (100)				
	Lycaenidae	2	2 (100)		2	2 (100)		1	1 (100)	
	Macroglossidae	1	1 (100)		1	1 (100)		1	1 (100)	
	Noctuidae	11	5 (45)	1 (9)	10	4 (40)	1 (10)	1	1 (100)	
	Nymphalidae	2	2 (100)		2	2 (100)		2	2 (100)	
	Papillionidae	1	1 (100)		1	1 (100)				
	Pieridae	1		1 (100)				1		1 (100)
	Pterophoridae	1			1					
	Sphingidae	2	2 (100)		2	2 (100)		1	1 (100)	
Passeriformes	Ploceidae	1		1 (100)	1		1 (100)			
	Pycnonotidae	1		1 (100)	1		1 (100)			
	Zosteropidae	1	1 (100)		1	1 (100)		1	1 (100)	
Squamata	Gekkonidae	1	1 (100)		1	1 (100)		1	1 (100)	

APPENDIX V continued

Order	Family	Total			Restored			Unrestored		
		Number of species	Number (%) of native species	Number (%) of introduced species	Number of species	Number (%) of native species	Number (%) of introduced species	Number of species	Number (%) of native species	Number (%) of introduced species
Coleoptera	Cerambycidae	4	1 (25)		3	1 (33)		4	1 (25)	
	Chrysomelidae	5		1 (20)	2		1 (50)	4		1 (25)
	Coccinellidae	1			1					
	Cucujidae	1		1 (100)	1		1 (100)	1		1 (100)
	Curculionidae	1						1		
	Melyridae	2			2			2		
	Mordellidae	3			2			3		
	Nitidulidae	1						1		
	Scirtidae	2			2			2		
Diptera	Acalyptrate	1			1					
	Agromyzidae	2	1 (50)	1 (50)	1		1 (100)	1	1 (100)	
	Anthomyiidae	1	1 (100)		1	1 (100)				
	Bombyliidae	1	1 (100)		1	1 (100)		1	1 (100)	
	Calliphoridae	2	1 (50)	1 (50)	2	1 (50)	1 (50)	2	1 (50)	1 (50)
	Chironomidae	1			1					
	Dolichopodidae	1			1					
	Drosophilidae	5		2 (40)	5		2 (40)			
	Ephydridae	2		1 (50)	2		1 (50)			
	Fanniidae	1		1 (100)	1		1 (100)	1		1 (100)
	Lauxaniidae	6	4 (67)		6	4 (67)		4	3 (75)	
	Limoniidae	2			2					
	Muscidae	13	6 (46)	5 (38)	10	3 (30)	5 (50)	11	6 (55)	5 (45)
	Mycetophilidae	1	1 (100)		1	1 (100)		1	1 (100)	
	Psyllidae	1			1					
	Sarcophagidae	1		1 (100)	1		1 (100)	1		1 (100)
	Scatopsidae	1			1			1		
	Sepsidae	1		1 (100)	1		1 (100)			
	Simuliidae	2		1 (50)	2		1 (50)	1		1 (100)
	Syrphidae	13	5 (38)	6 (46)	12	5 (42)	5 (42)	11	5 (45)	6 (55)
	Tachinidae	5	2 (40)		4	1 (25)		4	2 (50)	
	Tephritidae	5		3 (60)	5		3 (60)	3		2 (75)
	Unknown	3			1			2		

APPENDIX VI

Flowering phenology of 50 plant species which occurred at both sites, (R) the restored CMA and (U) the unrestored site. Flowering was recorded from August 2003 to March 2004. The height of the bars indicates the proportional number of floral units in a given fortnight in relation to the total number of floral units counted over the entire season. The solid line underneath the bars represents the total flowering time of each species independent on whether floral units were counted in a given fortnight. The dashed line indicates that one or two individuals were recorded in blossom, i.e. it reflects the beginning or the end of the flowering season of a species. Plant species were sorted according to their start of flowering to facilitate comparison of plant species, which overlapped in flowering time.


Antirhea borbonica
U
R
Aphloia theiformis
U
R
Psiadia terebinthina
U
R
Phyllanthus phillyreifolius
U
R
Croton fothergillifolius
U
R
Erythroxylon macrocarpum
U
R
Claoxylon linostachys
U
R
Trochetia blackburniana
U
R
Dodonaea viscosa
U
R
Toddalia asiatica
U
R
Stillingia lineata
U
R
Molinaea alternifolia
U
R
Chassalia coriacea
U
R
Sideroxylon cinereum
U
R
Flagellaria indica
U
R
Bertiera zaluzania
U
R
A
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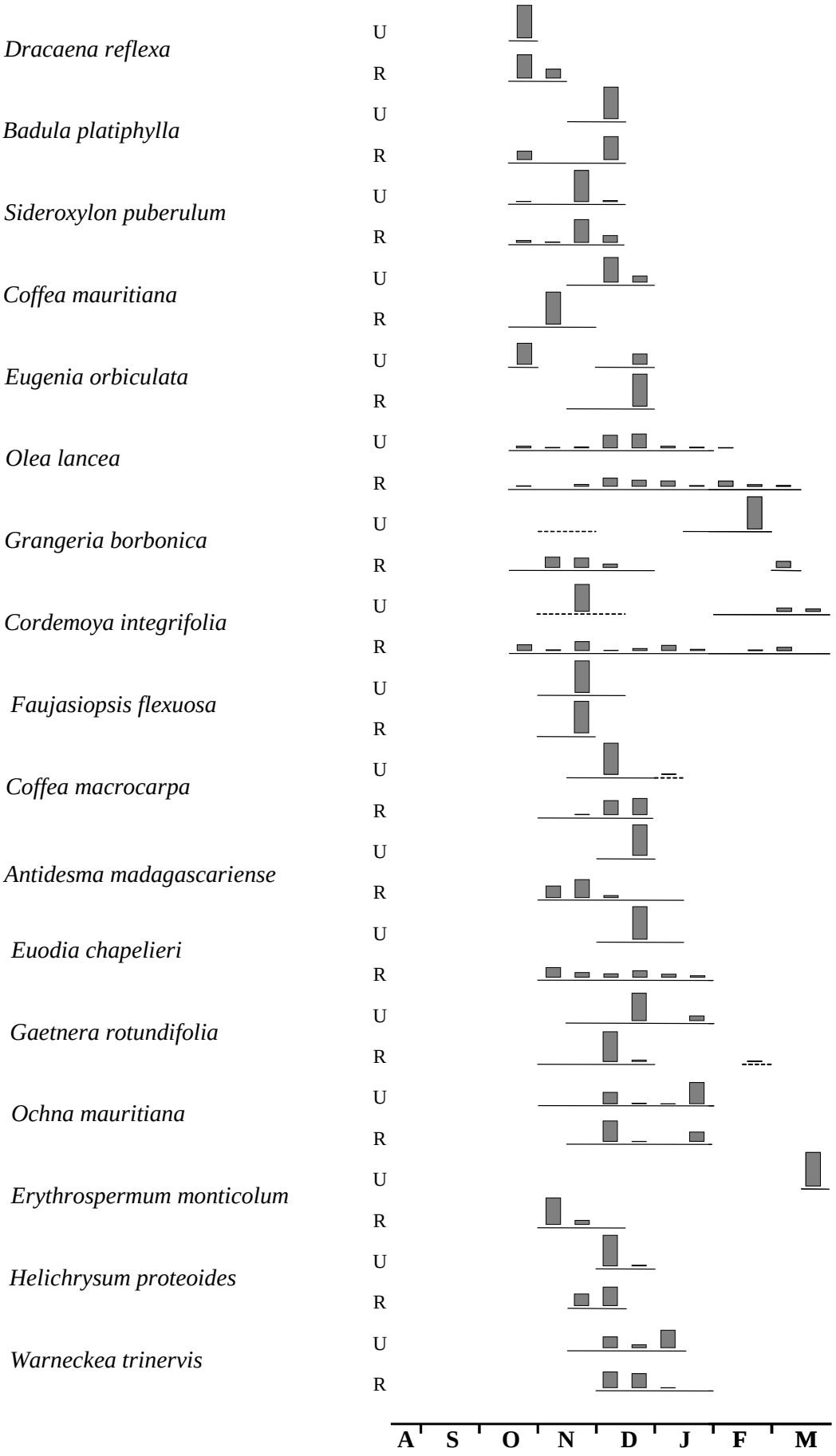
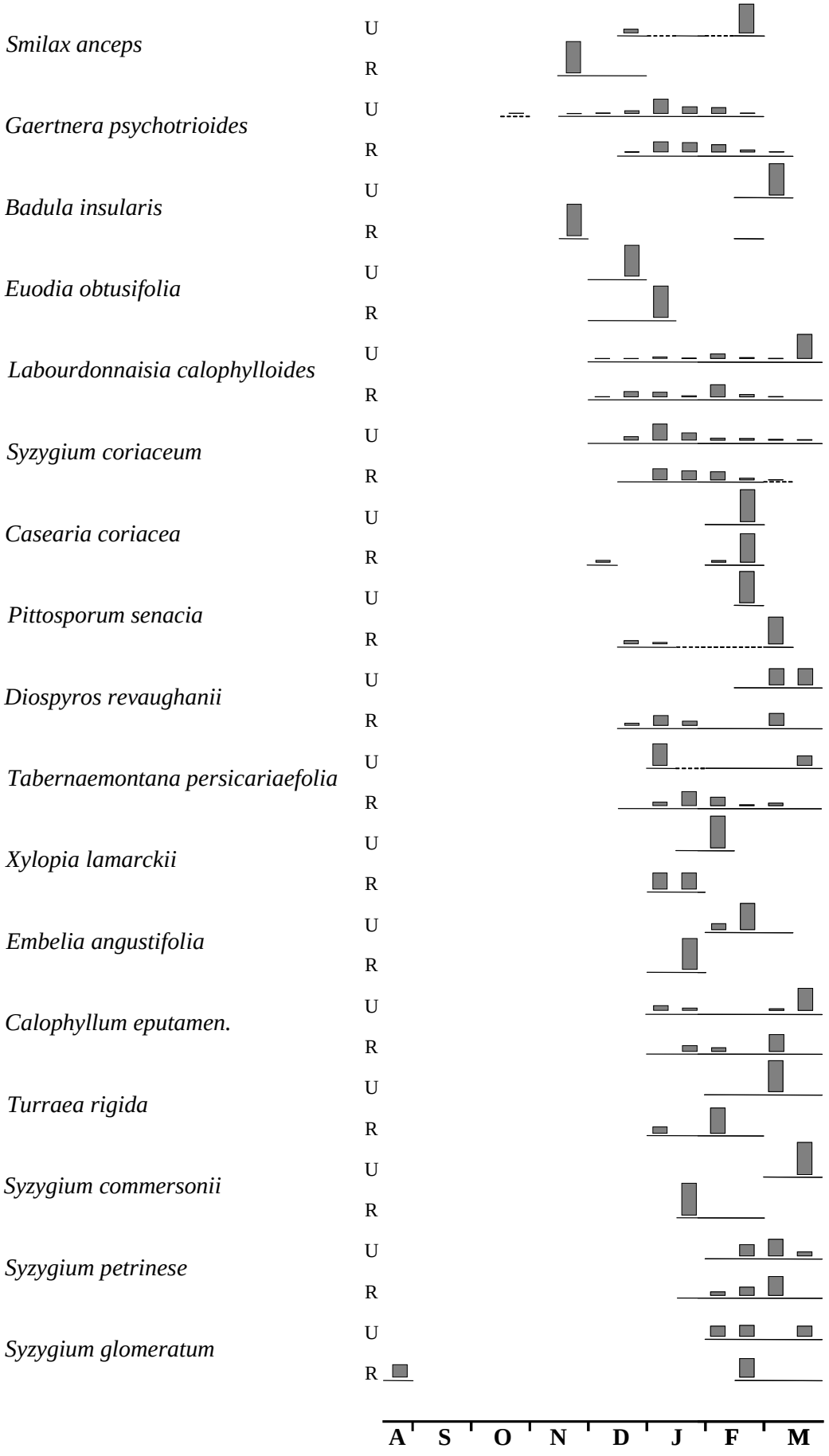
M


Dracaena reflexa
Badula platiphylla
Sideroxylon puberulum
Coffea mauritiana
Eugenia orbiculata
Olea lancea
Grangeria borbonica
Cordemoya integrifolia
Faujasiopsis flexuosa
Coffea macrocarpa
Antidesma madagascariense
Euodia chapelieri
Gaetnera rotundifolia
Ochna mauritiana
Erythrospermum monticolum
Helichrysum proteoides
Warneckea trinervis
U
R
A S O N D J F M


Smilax anceps
U
R
Gaertnera psychotrioides
U
R
Badula insularis
U
R
Euodia obtusifolia
U
R
Labourdonnaisia calophylloides
U
R
Syzygium coriaceum
U
R
Casearia coriacea
U
R
Pittosporum senacia
U
R
Diospyros revaughanii
U
R
Tabernaemontana persicariaefolia
U
R
Xylopia lamarckii
U
R
Embelia angustifolia
U
R
Calophyllum eputamen.
U
R
Turraea rigida
U
R
Syzygium commersonii
U
R
Syzygium petrinese
U
R
Syzygium glomeratum
U
R
A S O N D J F M

APPENDIX VII

Independent *t*-test of fruit size (diameter) and fruit weight for several common plant species in the restored CMA and unrestored area of Pétrin. Between three and five fruits were collected randomly from n individual plants and means of each plant were used in the analysis.
*p <0.05, **$p \leq 0.001$, *** $p < 0.0001$ after sequential Bonferroni corrections.

Plant species	Plant family	Fruit trait	*df*	*t*
Antidesma madagascariensis	Euphorbiaceae	Size	15	5.29***
		Weight	n.a.	n.a.
Aphloia theiformis	Flacourtiaceae	Size	11	3.32**
		Weight	11	1.3*
Casearia coriacea	Flacourtiaceae	Size	n.a.	n.a.
		Weight	12	3.56**
Chassalia coriaceae	Rubiaceae	Size	22	2.32*
		Weight	21	1.36
Coffea macrocarpa	Rubiaceae	Size	11	4.24**
		Weight	11	6.46***
Croton fothergillifolius	Euphorbiaceae	Size	24	3.89**
		Weight	n.a.	n.a.
Draceana reflexa	Draceanaceae	Size	8	4.72**
		Weight	8	3.48**
Erythroxylon macrocarpum	Erythroxylaceae	Size	9	0.49
		Weight	15	1.68
Eugenia orbiculata	Myrtaceae	Size	17	1.38
		Weight	17	1.04
Flagellaria indica	Flagellariaceae	Size	24	1.13
		Weight	n.a.	n.a.
Gaertnera psychotrioides	Rubiaceae	Size	15	4.59***
		Weight	15	3.25**
Mimusops erythroxylon	Sapotaceae	Size	8	1.03
		Weight	8	1.88
Ochna mauritiana	Ochnaceae	Size	19	6.08***
		Weight	20	3.78**
Stillingia lineata	Euphorbiaceae	Size	11	0.88
		Weight	11	0.91
Syzygium coriaceum	Myrtaceae	Size	14	0.45
		Weight	14	0.19

APPENDIX VII continued

Non-parametric Mann-Whitney *U*-test of number of seeds per fruit for several common plant species in the restored and unrestored site at Pétrin. Between three and five fruits were collected randomly from *n* individual plants and means of each plant were used for the analysis. Plant species with equal number of seeds per fruit in both sites were excluded. Statistically significant *p* values (<0.05) are indicated in bold.

Plant species	Plant family	*n*	*U*	*p*
Aphloia theiformis	Flacourtiaceae	13	1.0	**0.002**
Casearia coriacea	Flacourtiaceae	14	71.0	0.062
Coffea macrocarpa	Rubiaceae	13	8.0	**0.050**
Croton fothergillifolius	Euphorbiaceae	25	26.5	**0.002**
Draceana reflexa	Draceanaceae	10	2.5	**0.018**
Eugenia orbiculata	Myrtaceae	20	24.0	0.133
Stillingia lineata	Euphorbiaceae	13	17.0	0.55

APPENDIX VIII

Flower visitors of Pétrin (excluding G & L).

A: *Phelsuma cepediana* (Gekkonidae) on *Molinaea alternifolia* (Sapindaceae)

B: *Apis mellifera* (Apidae) on *Psiadia terebinthina* (Asteraceae)

C: *Paragus borbonicus* (Syrphidae) on *Dodonaea viscose*

D: *Eurytonidae sp 1* (Chalcidoidae) on *Phyllanthus phillyreifolius* (Euphorbiaceae)

E: *Phelsuma cepediana* on *Labourdonnaisia calophylloides* (Sapotaceae, photograph by D. M. Hansen)

F: Spider on *Syzygium coriaceum* (Myrtaceae)

G: *Phelsuma ornata* (Gekkonidae) on *Gastonia mauritiana* (Araliaceae, on Ile aux Aigrettes)

H: *Eristalinus flaveolus* (Syrphidae) on *Stillingia lineata* (Euphorbiaceae)

I: *Apis mellifera* on *Polyscias mauritiana* (Araliaceae)

J: *Panara naso* (Hesperidae)

K: *Phelsuma cepediana* and *Apis mellifera* feeding on pollen of *Pandanus barklyi* (Pandanaceae)

L: *Zosterops mauritianus* (grey white-eye, Zosteropidae) on *Syzygium mamillatum* (Myrtaceae, at Brise Fér)

M: *Orthellia albigena* (Muscidae) on *Stillingia lineata*

N: *Stomorhina lunata* (Calliphoridae) on *Chassalia coriacea* (Rubuiaceae)

O: *Polistes hebraeus* (Vesperidae) on *Sideroxylon puberulum* (Sapotaceae)

P: *Zosterops chloronthos* (Zosteropidae) on *Sideroxylon cinereum* (Sapotaceae, photograph by D. M. Hansen)

Q: *Phelsuma cepediana* (female) on *Syzygium petrinense* (Myrtaceae)

R: *Villa unifasciata* on *Psidium cattleianum* (Myrtaceae)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APPENDIX IX

A selection of flowering plant species at Pétrin.

A: *Turraea rigida* (Meliaceae, photograph by D. M. Hansen)

B: *Colea colei* (Bignoniaceae)

C: *Diospyros revaughanii* (Ebenaceae)

D: *Casearia coriacea* (Flacourtiaceae)

E: *Xylopia lamarckii* (Annonaceae)

F: *Chassalia capitata* (Rubiaceae)

G: *Coffea macrocarpa* (Rubiaceae)

H: *Aphloia theiformis* (Flacoutaceae)

I: *Trochetia blackburniana* (Malvaceae)

J: *Helichrysum proteioides* (Asteraceae)

K: *Embelia angustifolia* (Myrsinaceae)

L: *Syzygium venosum* (Myrtaceae)

M: *Ochna mauritiana* (Ochnaceae)

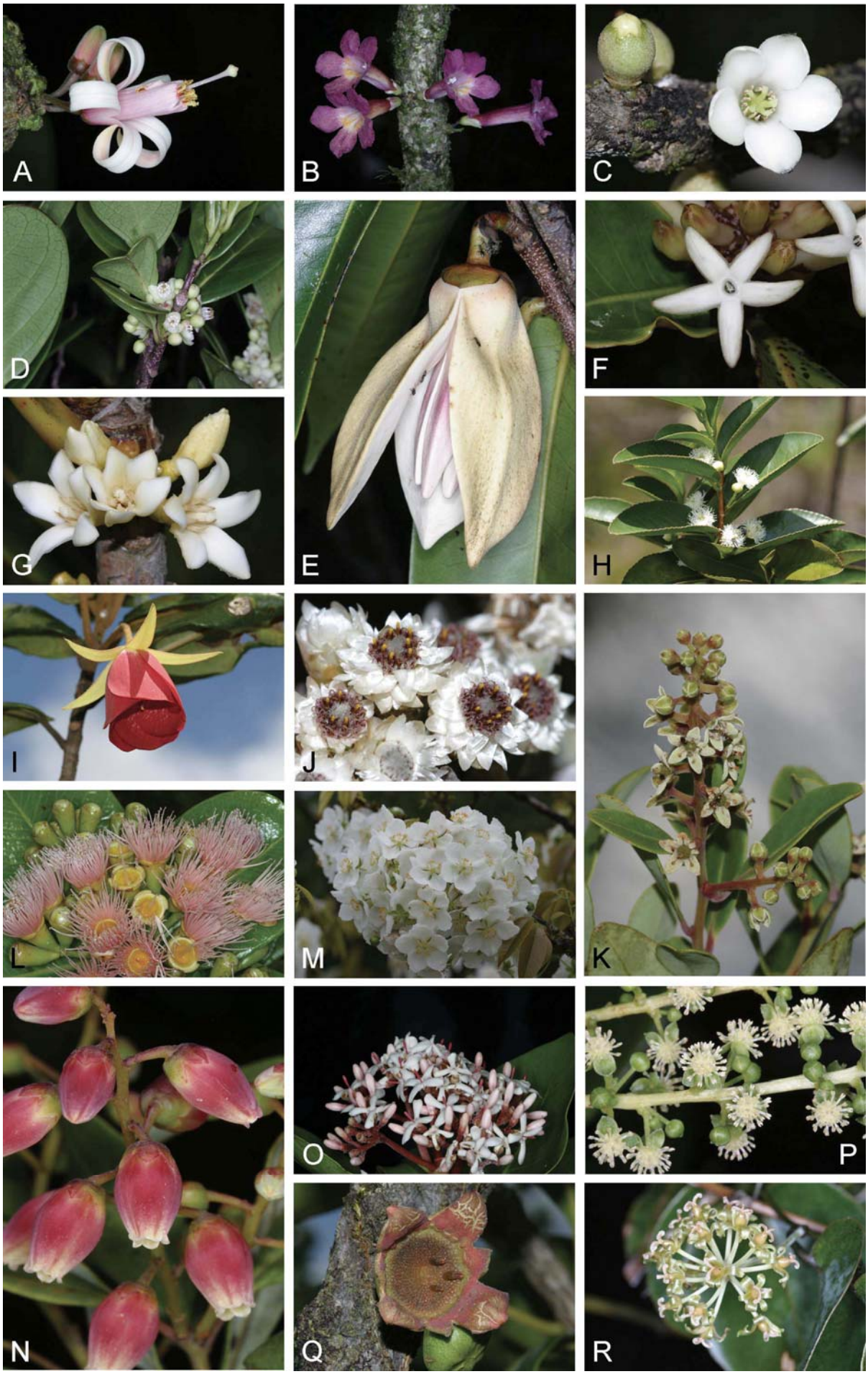
N: *Agauria salicifolia* (Ericaceae)

O: *Myonima violacea* (Rubiaceae)

P: *Claoxylon linostachys ssp. brachyphyllum* (Euphorbiaceae)

Q: *Tambourissa peltata* (female flower, with *Zaprionus tuberculatus*, Drosophilidae)

R: *Smilax anceps* (Smilacaceae)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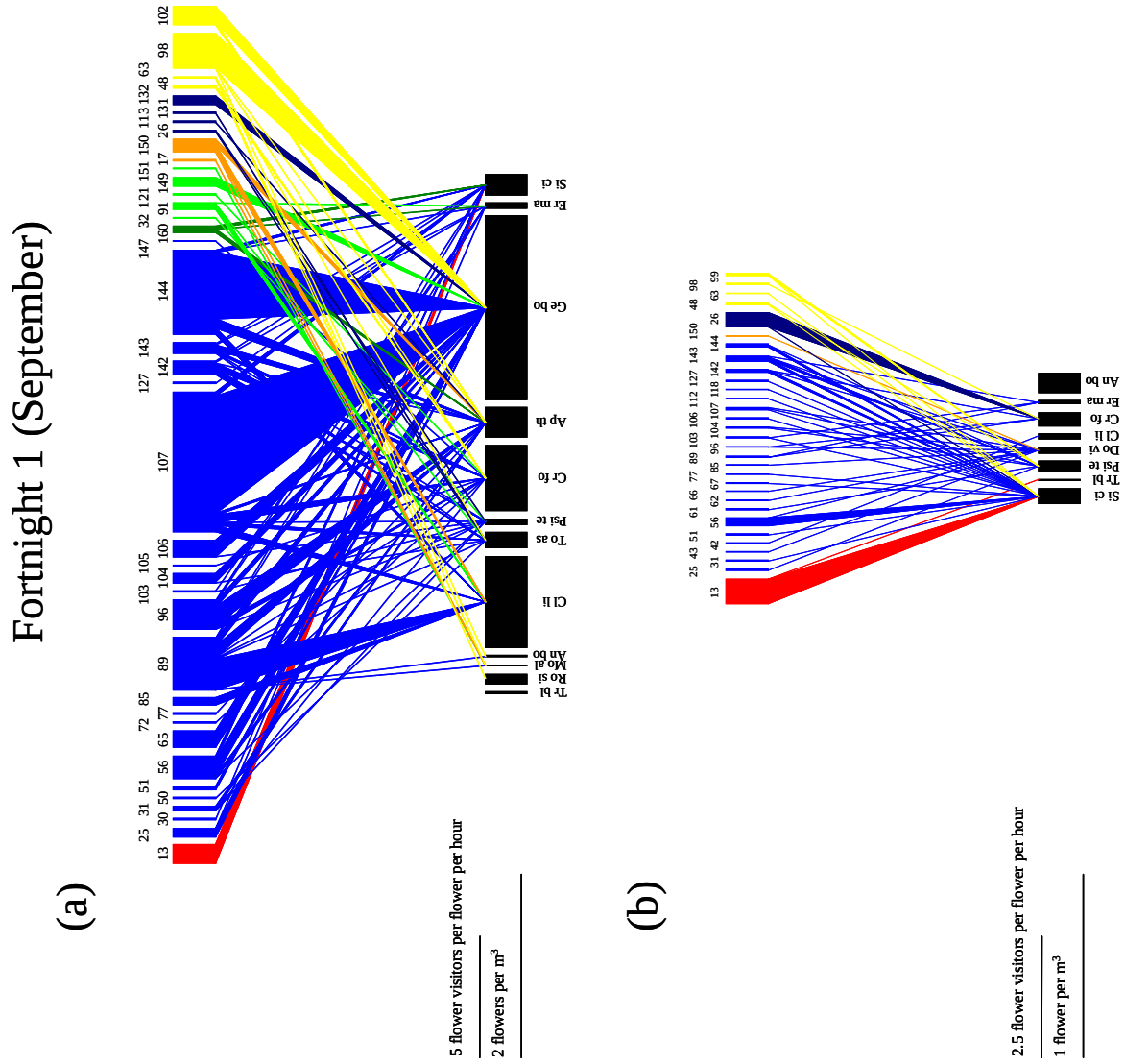
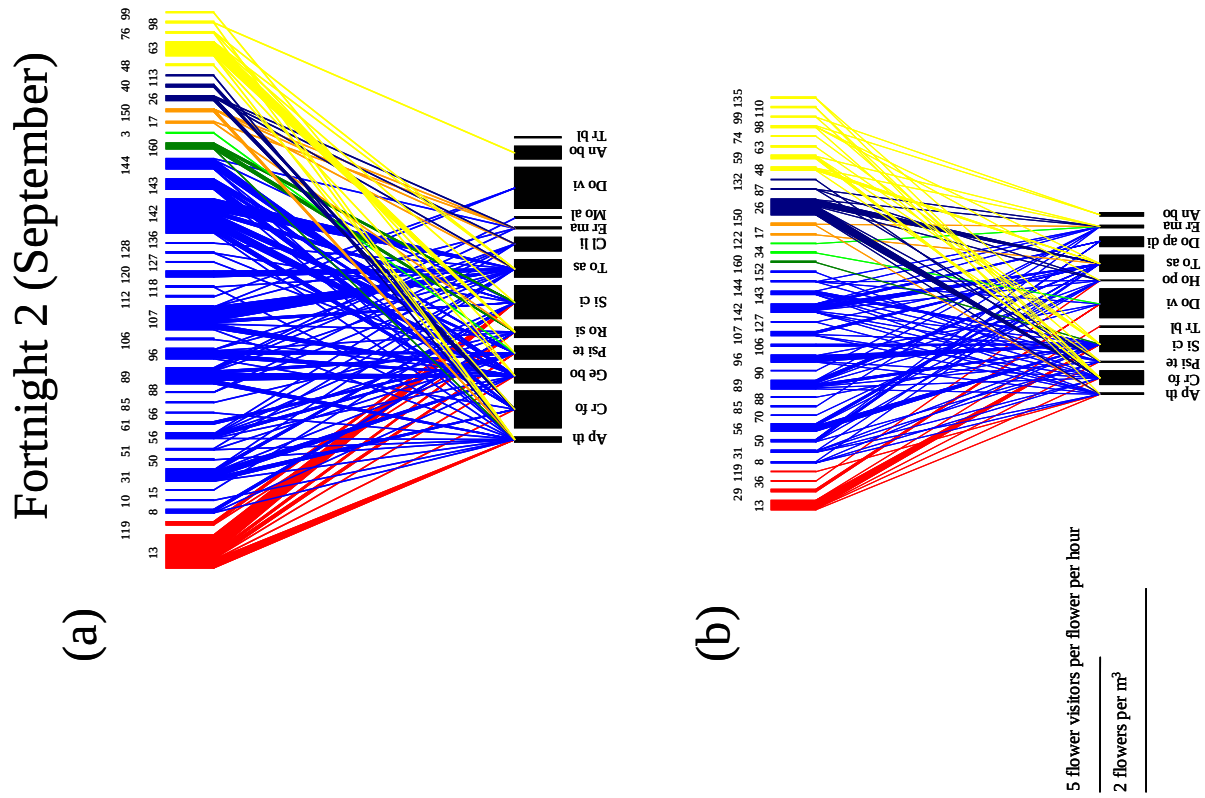
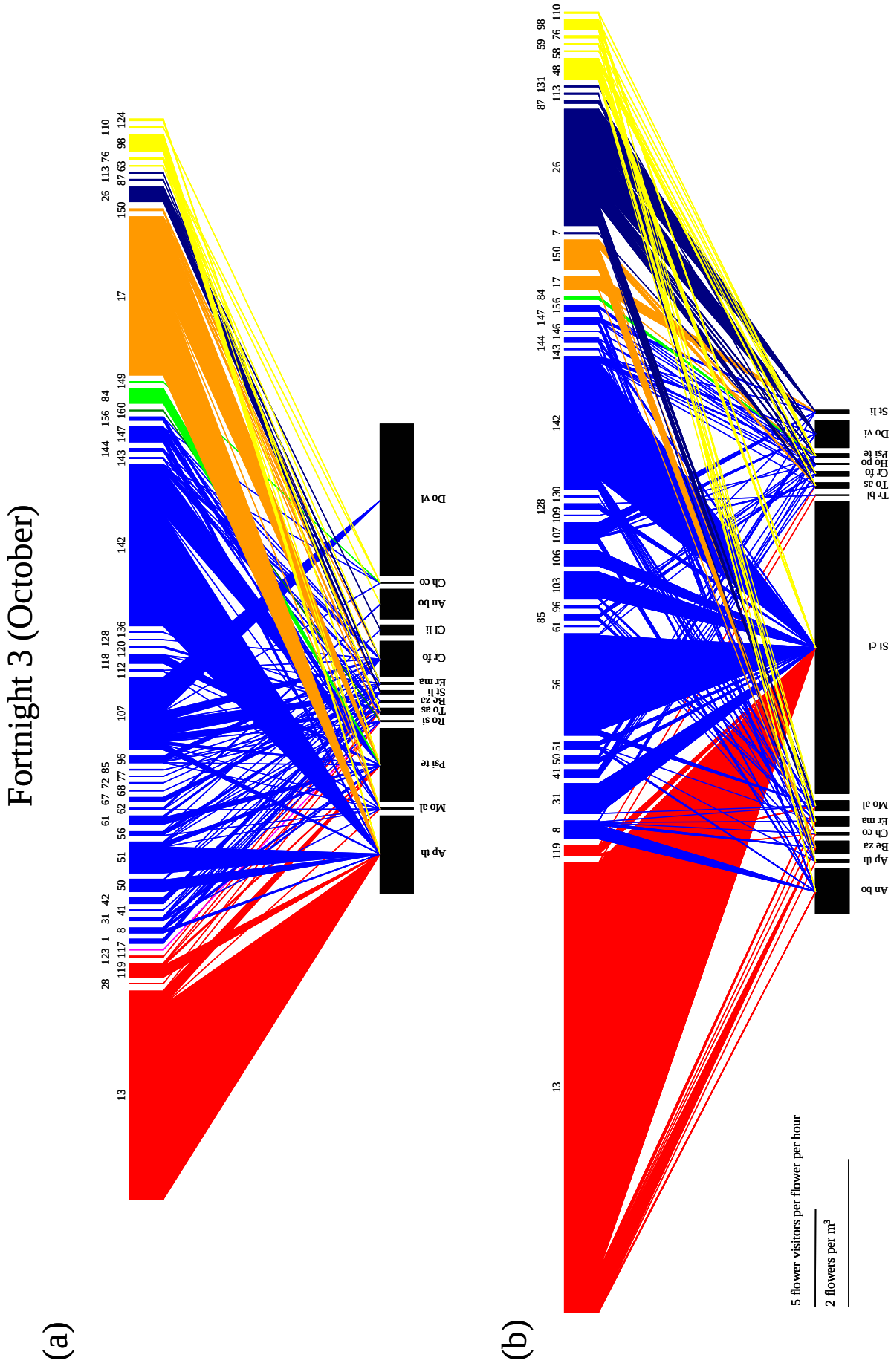
APPENDIX X

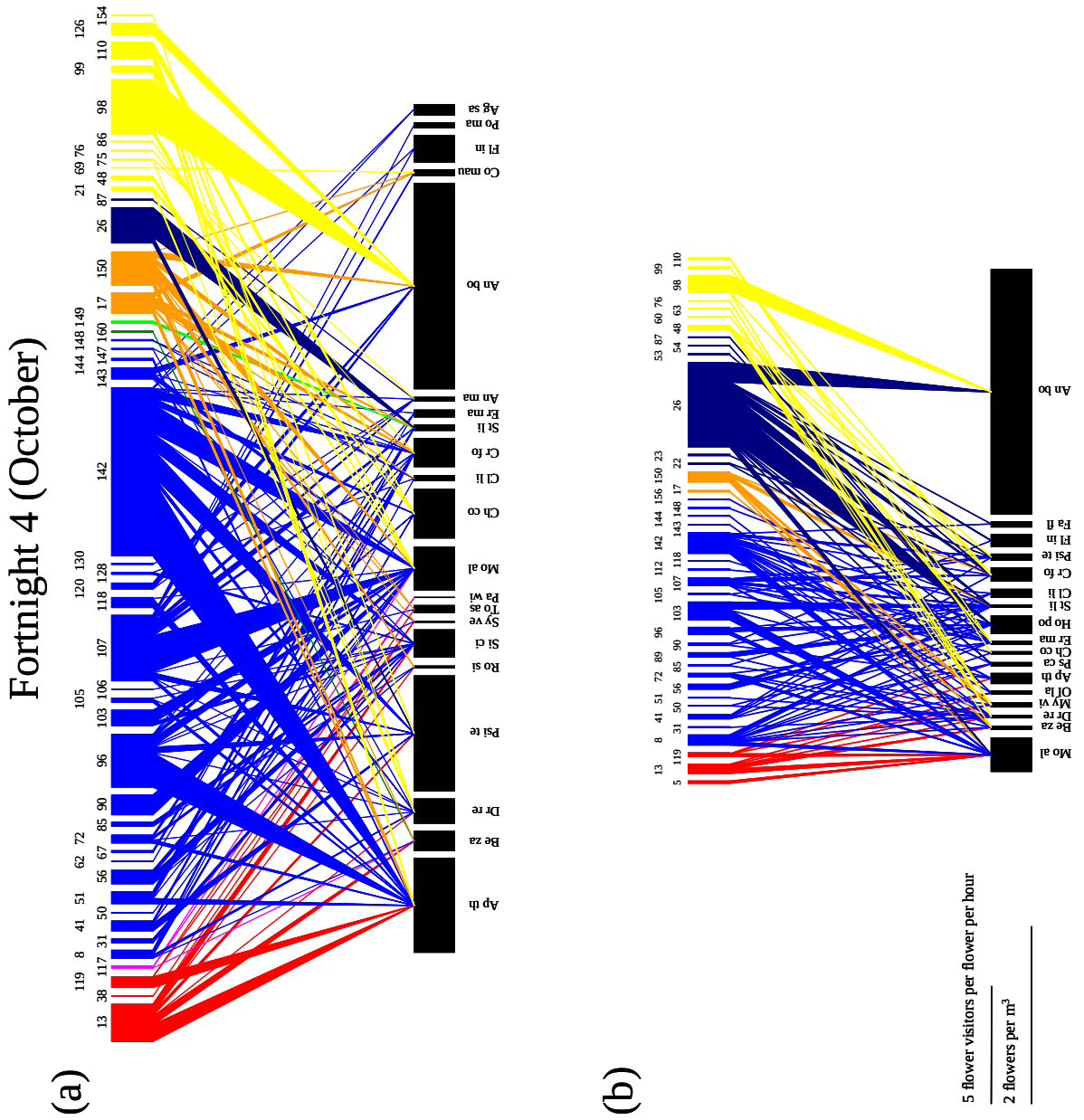
(pp 238–250)

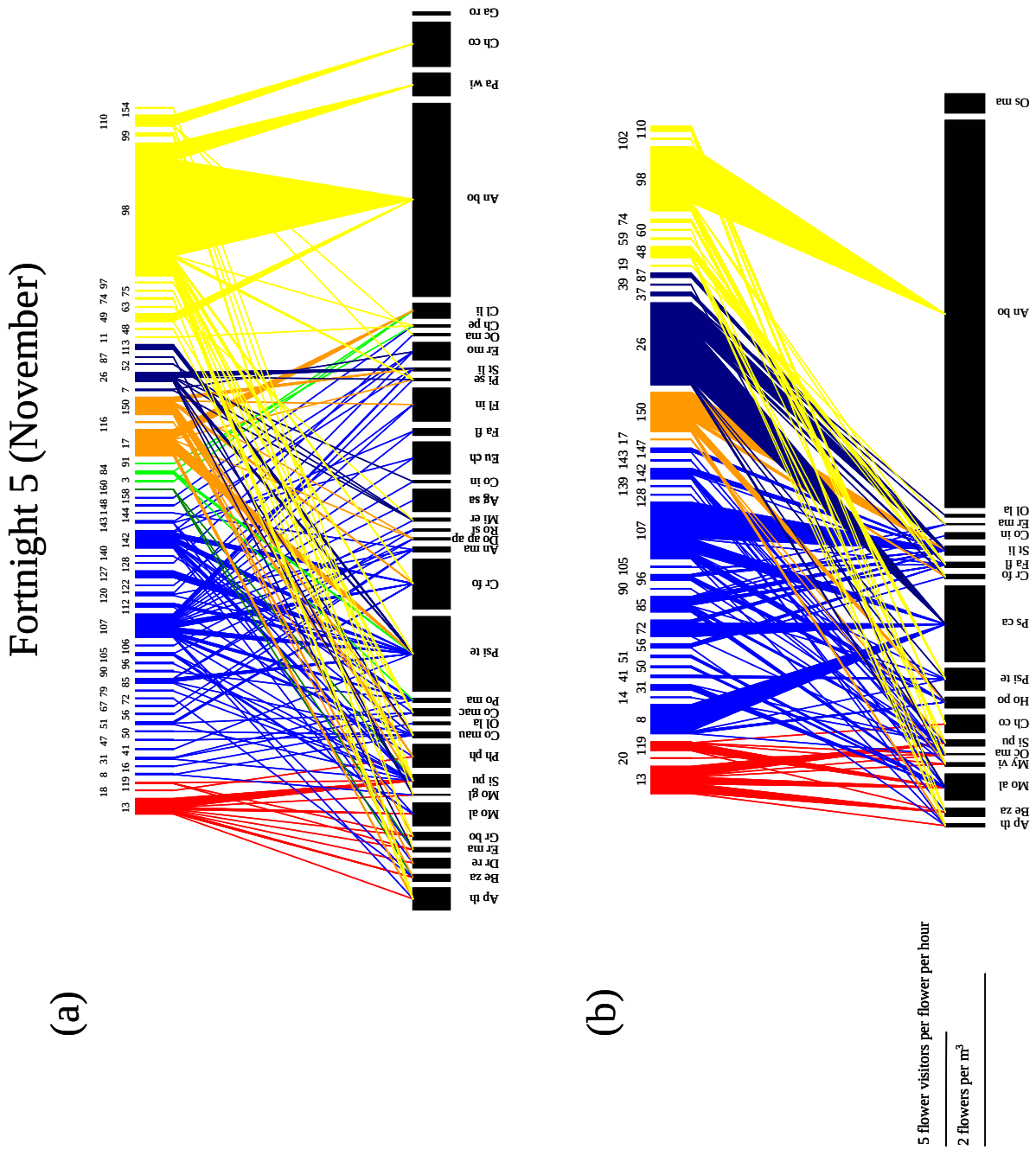
Quantified visitation webs for plant–pollinator communities in the (a) restored and (b) unrestored site. Visitor species are depicted as rectangles at the top and plant species are shown at the bottom. The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantified visitation rate (interaction strength) between an interacting pair of species. Webs are drawn to the same scale (except fortnight 1 unrestored and 13 both sites). Red: Hymenoptera, pink: Gekkonidae, light blue: Diptera, dark green: Aves, light green: Hemiptera, orange: Formicidae, dark blue: Coleoptera, and yellow: Lepidoptera. For species codes see Appendices I & II.

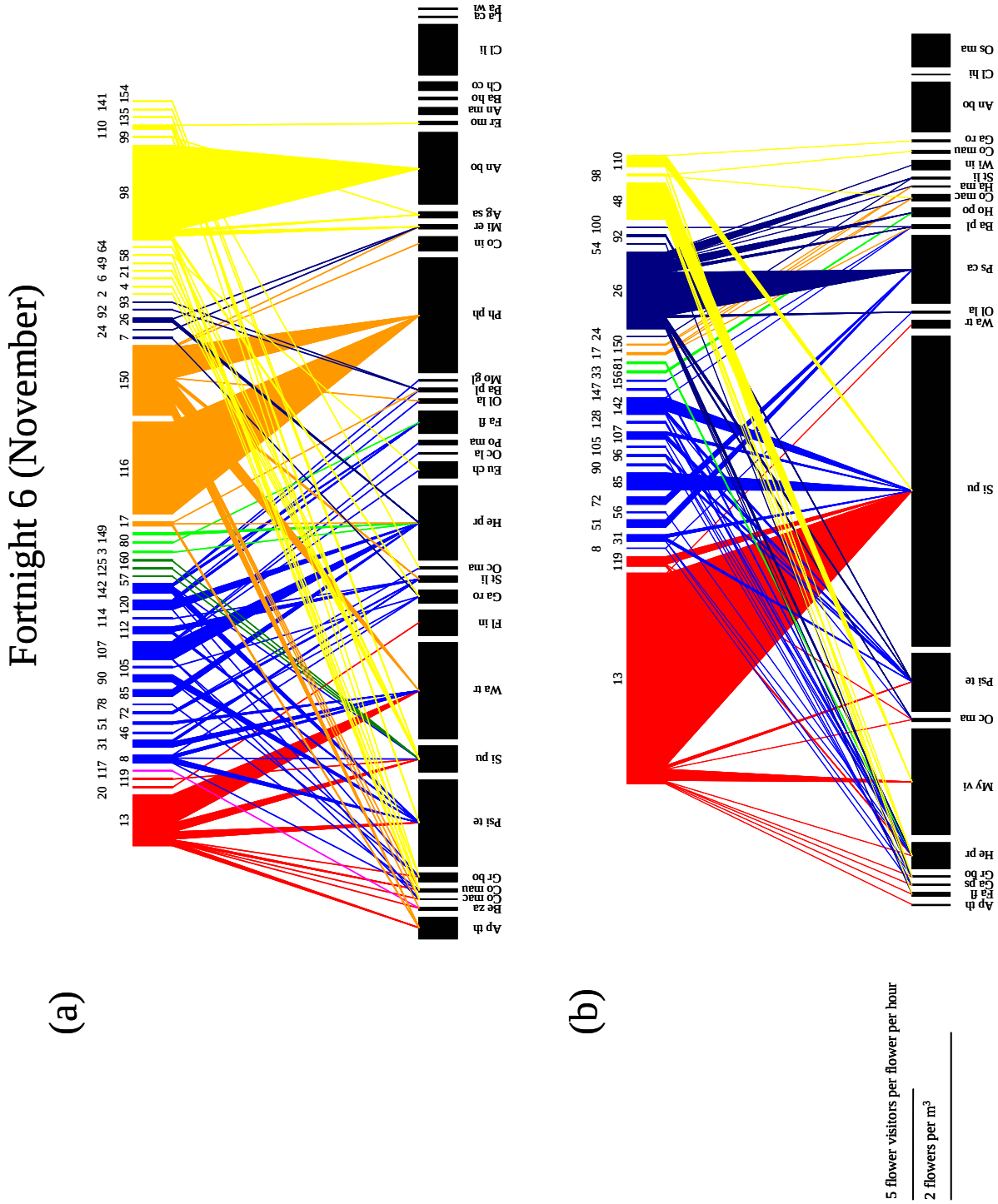



Fortnight 2 (September)
(a)
13 119 10 31 8 15 51 50 61 56 85 66 88 89 106 96 107 112 120 128 118 127 136 142 143 144 3 150 160 17 26 113 40 48 63 76 99 98
Ap th
Cr fo
Ge bo
Psi le
Ro si
Si ci
To as
Cl li
Er ma
Mo al
Do vi
An bo
Tr bl
(b)
29 119 31 36 8 50 56 70 85 88 89 90 96 106 107 127 142 143 144 160 152 34 17 122 150 26 87 132 59 48 63 74 98 110 99 135
Ap th
Cr fo
Psi le
Si ci
Tr bl
Do vi
Ho po
To as
Do ap di
Er ma
An bo
5 flower visitors per flower per hour
2 flowers per m3


Fortnight 3 (October)
(a)
(b)
Ap th
Mo al
Psi te
Ro si
To as
Be za
St li
Er ma
Cr fo
Cl li
An bo
Ch co
Do vi
Si ci
Tr bl
Ha po
5 flower visitors per flower per hour
2 flowers per m3

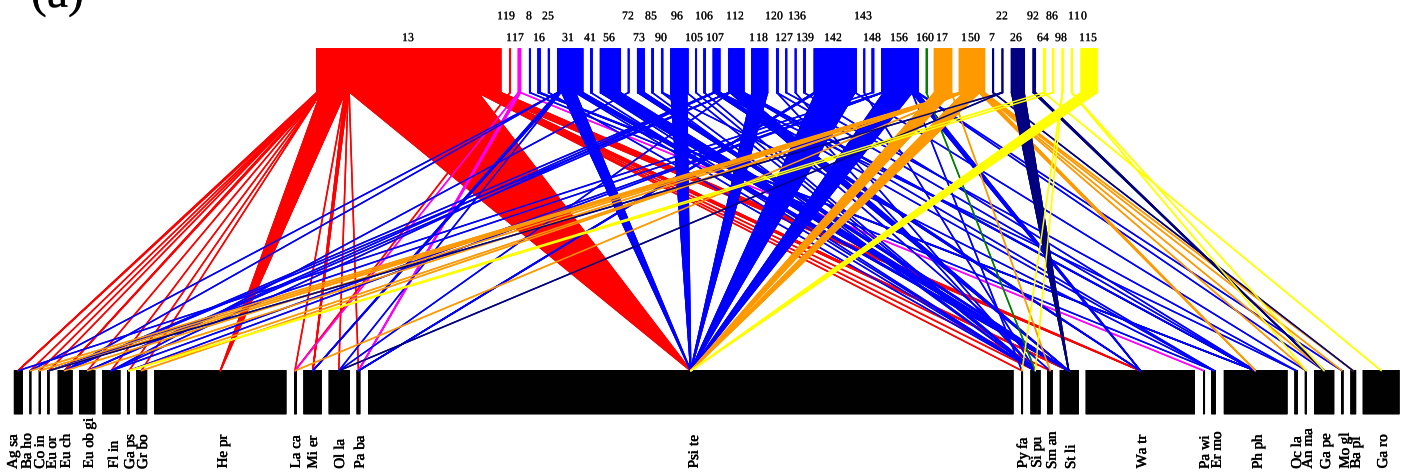

(a)
Fortnight 4 (October)
Ap th
Be za
Dr re
Ps te
Ro si
Si ci
Sy ve
To as
Pa wi
Mo al
Ch co
Cl li
Cr fo
Sl li
Br ma
An ma
An bo
Co mau
Fl in
Po ma
Ag sa
(b)
Mo al
Be za
Dr re
My vi
Ol la
Ap th
Ps ca
Ch co
Er ma
Ho po
Sl li
Cl li
Cr fo
Ps te
Fl in
Fa fi
An bo
5 flower visitors per flower per hour
2 flowers per m3


Fortnight 5 (November)
(a)
(b)
5 flower visitors per flower per hour
2 flowers per m³

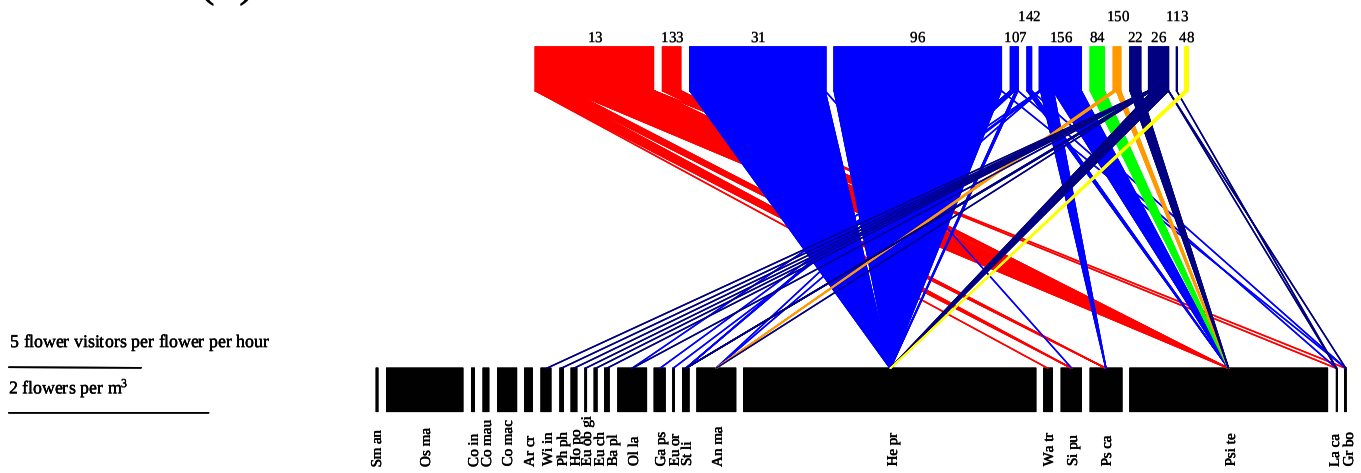

Fortnight 6 (November)
(a)
(b)
5 flower visitors per flower per hour
2 flowers per m3

Fortnight 7 (December)

(a)

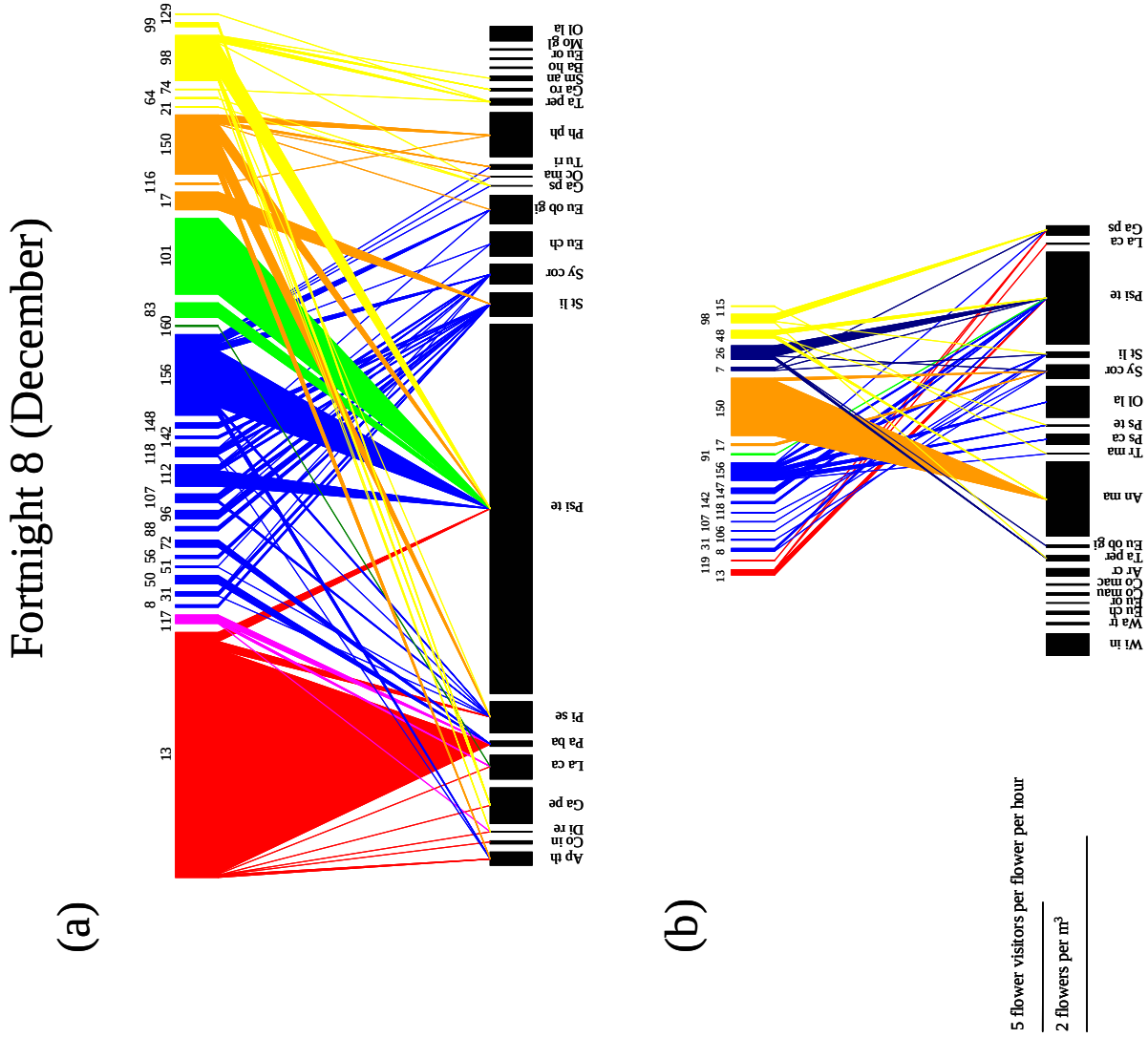


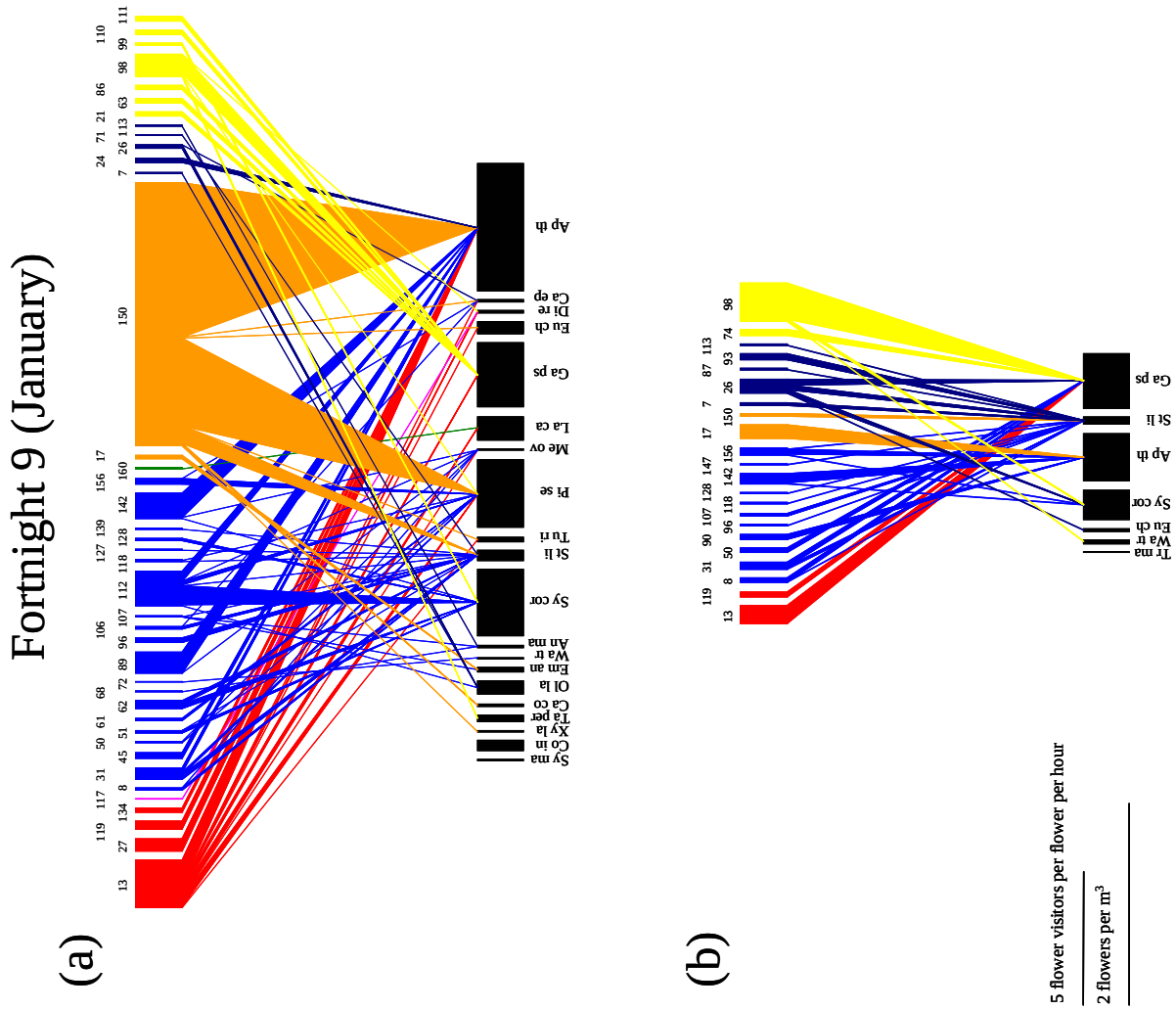
(b)

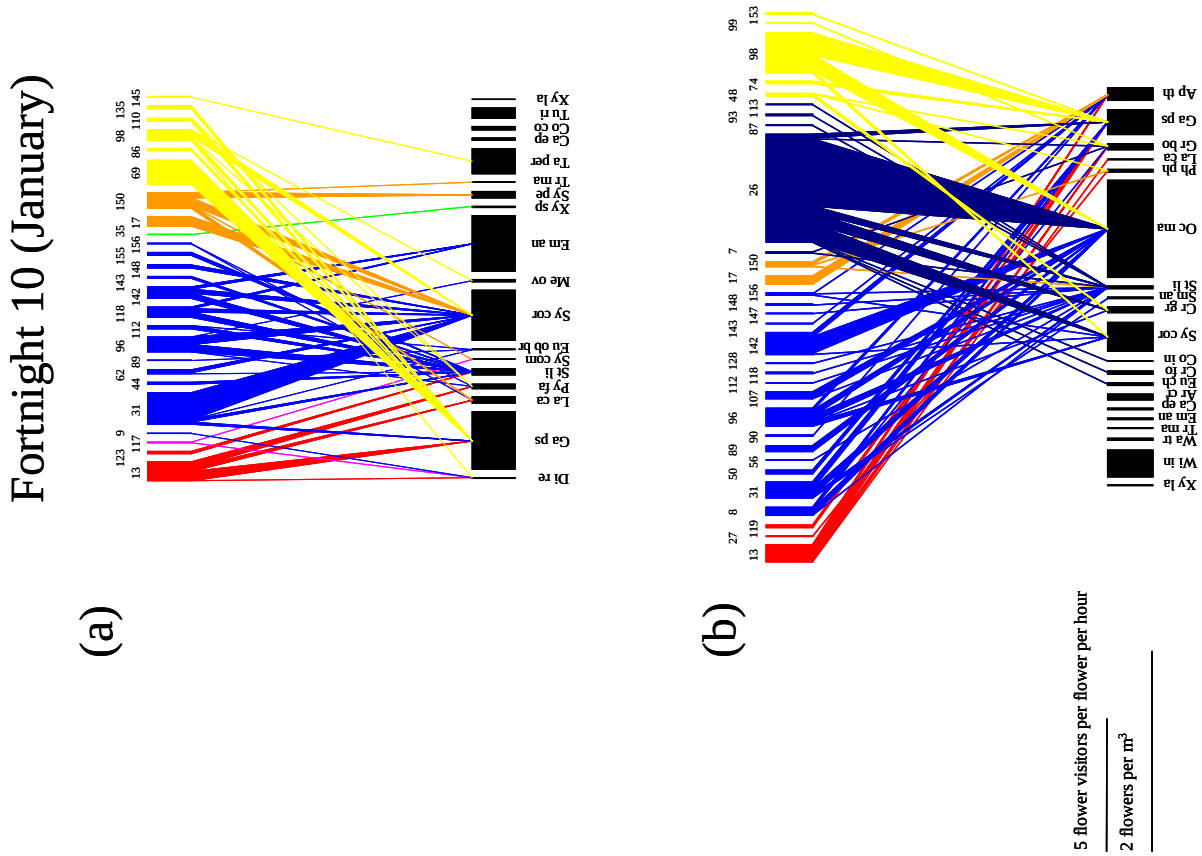


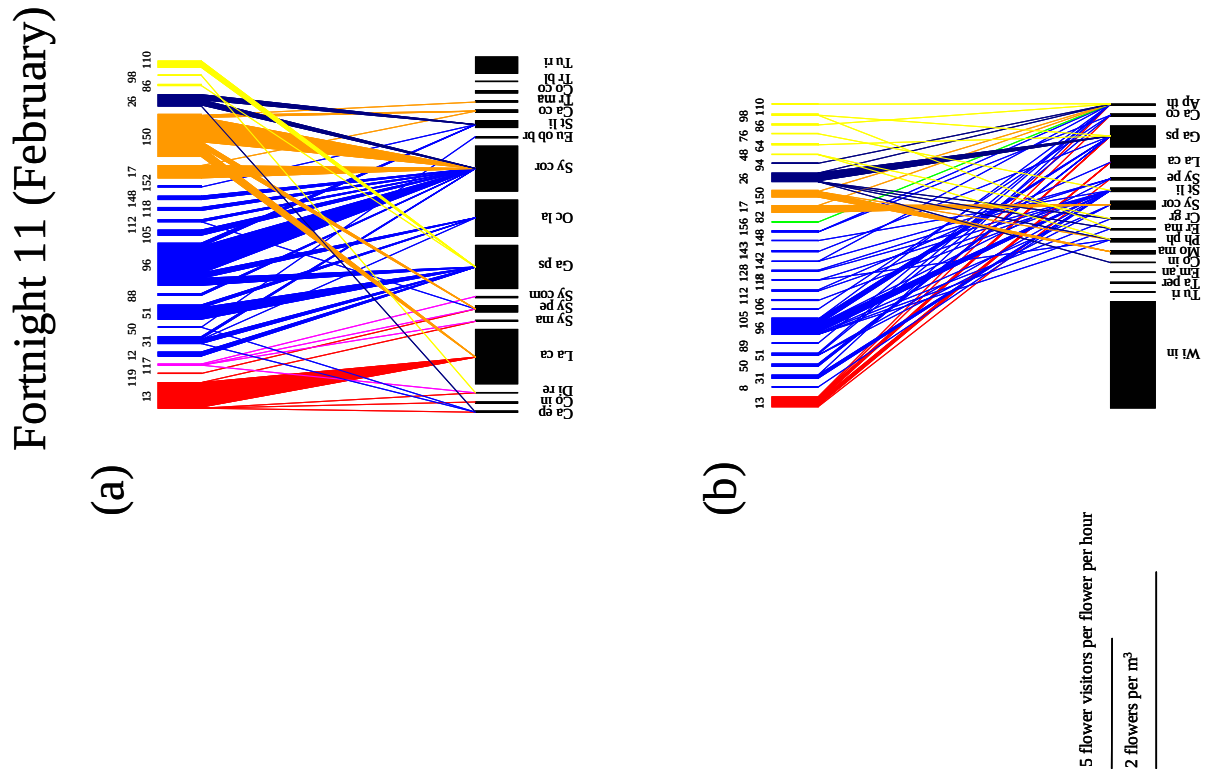
5 flower visitors per flower per hour

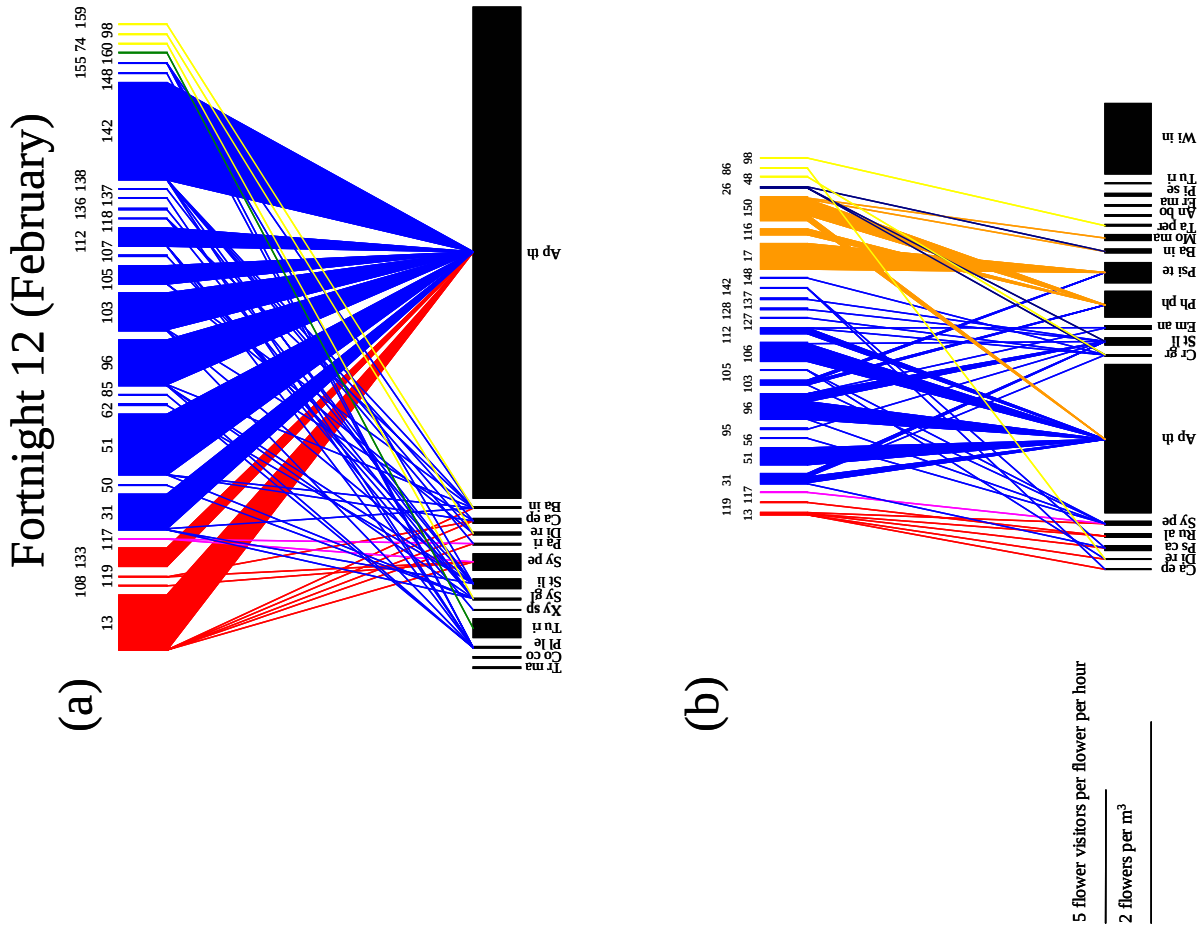
2 flowers per m^3

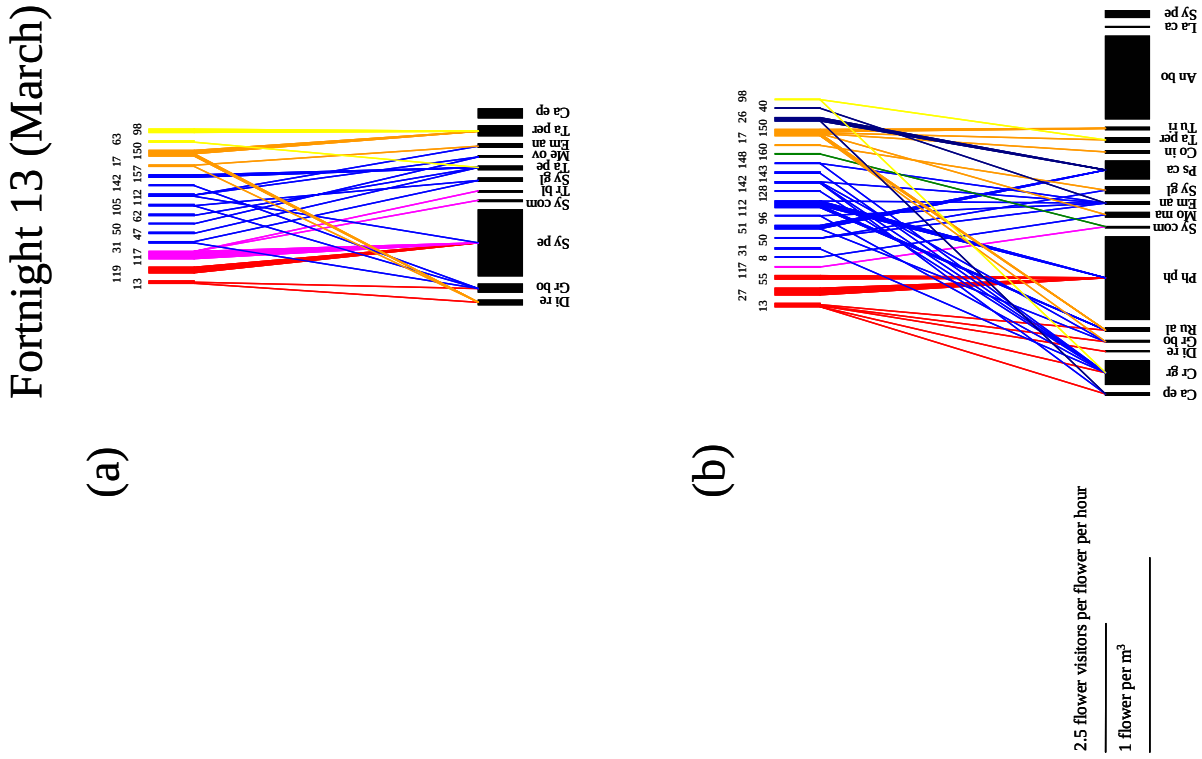

Fortnight 8 (December)
(a)
Ap th
Co in
Di re
Ga pe
La ca
Pa ba
Pi se
Psi te
St li
Sy cor
Eu ch
Eu ob gi
Ga ps
Oc ma
Tu ri
Ph ph
Ta per
Ga ro
Sm an
Ba ho
Eu or
Mo gl
Ol la
(b)
Wi in
Wa ri
Eu ch
Eu or
Co mau
Co mac
Ar cr
Ta per
Eu ob gi
An ma
Tr ma
Ps ca
Ps te
Ol la
Sy cor
St li
Psi te
La ca
Ga ps
5 flower visitors per flower per hour
2 flowers per m3


Fortnight 9 (January)
(a)
Ap th
Eu ch
Di re
Ca ep
Ga ps
La ca
Me ov
Pi se
St li
Tu ri
Sy cor
Ol la
Em an
Wa ir
An ma
Sy ma
Co in
Xy la
Ta per
Ca co
(b)
Ga ps
St li
Ap th
Sy cor
Tr ma
Wa ir
Eu ch
5 flower visitors per flower per hour
2 flowers per m3


Fortnight 10 (January)
(a)
(b)
5 flower visitors per flower per hour
2 flowers per m3

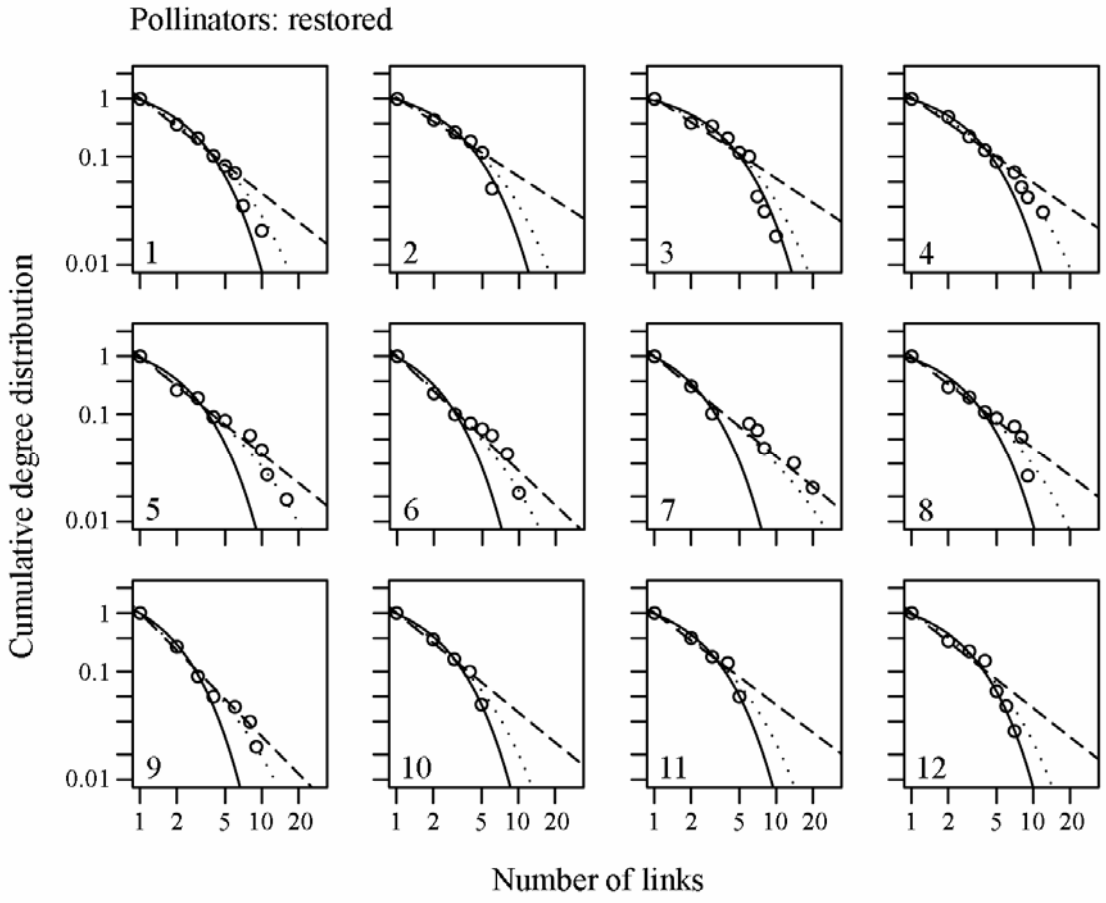

Fortnight 11 (February)
(a)
Ca ep
Co in
Di re
La ca
Sy ma
Sy pe
Sy com
Ga ps
Oc la
Sy cor
Eu ob br
St li
Ca co
Tr ma
Co co
Tr bl
Tu ri
(b)
Wi in
Tu ri
Ta per
Eu an
Co in
Mo ma
Ph ph
Fr ma
Cr gr
Sy cor
St li
Sy pe
La ca
Ga ps
Ca co
Ap in
5 flower visitors per flower per hour
2 flowers per m²


Fortnight 12 (February)
(a)
Ap th
Tr ma
Co co
Pl le
Tu ri
Xy sp
Sy gl
St il
Sy pe
Pa ri
Di re
Ca ep
Ba in
(b)
Ap th
Wi in
Ca ep
Di re
Ps ca
Ru al
Sy pe
Cr gr
St il
Em an
Ph ph
Psi te
Ba in
Mo ma
Ta per
Ag bo
Fe ma
Pl se
Tu ri
5 flower visitors per flower per hour
2 flowers per m3

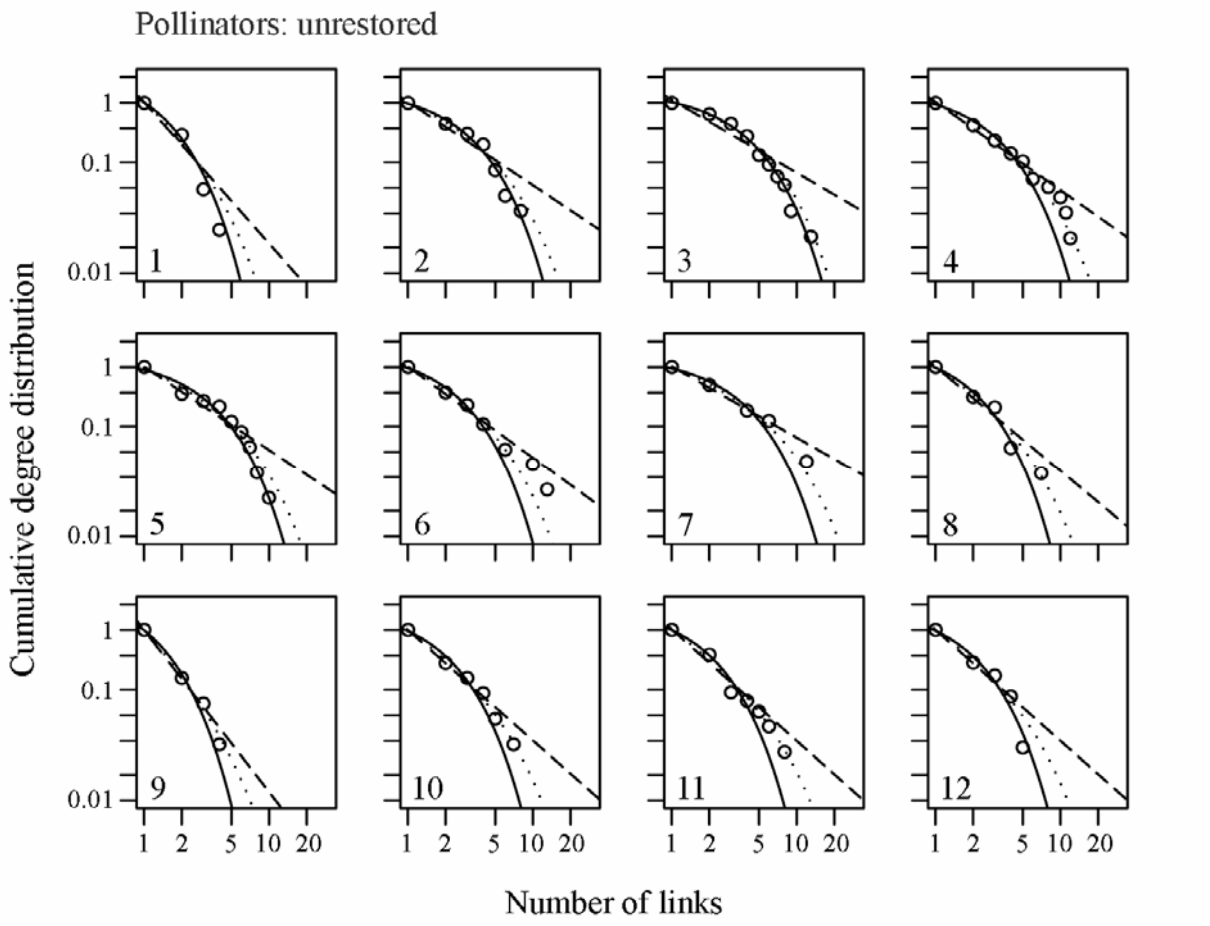

Fortnight 13 (March)
(a)
Ca ep
Ta per
Eu an
Me ov
Ta pe
Sy gl
Tr bl
Sy com
Sy pe
Gr bo
Di re
(b)
Ca ep
Cr gr
Gr bo
Di re
Ru al
Ph ph
Sy com
Mo ma
Eu an
Sy gl
Ps ca
Co in
Ta per
Tu ri
An bo
La ca
Sy pe
2.5 flower visitors per flower per hour
1 flower per m3

APPENDIX XI

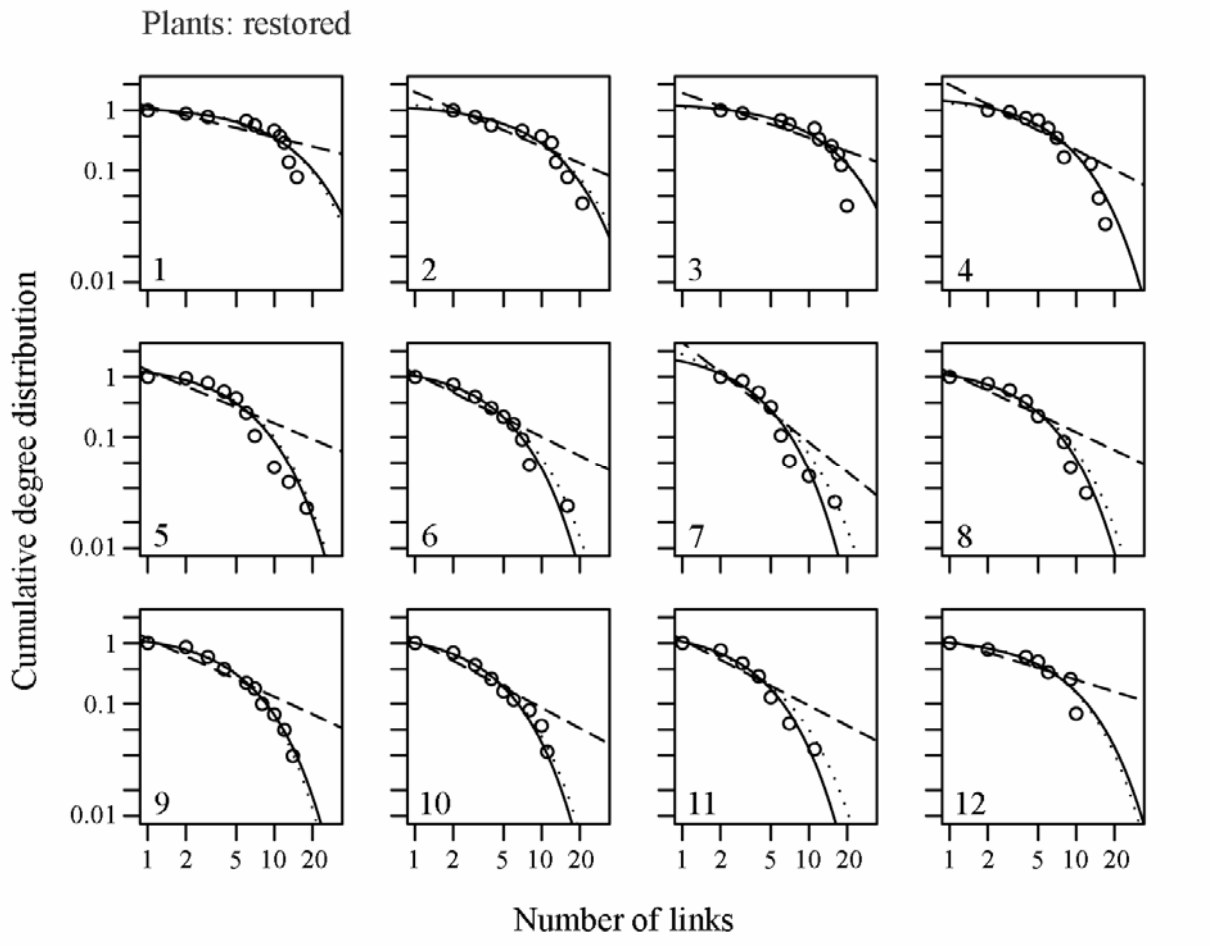
Cumulative distribution of number of links per species, *P*(k), for fortnightly plant–pollinator networks. Panels show the log-log plots of cumulative distribution of species 1, 2, 3 …, k links (circles), exponential fits (solid lines), power-law fits (dashed lines) and truncated power-law fits (dotted lines). Numbers in the panels represent the fortnight of the network from September 2003 (1) to beginning March 2004 (12). The last fortnight (13) was omitted due to few numbers of links per species.



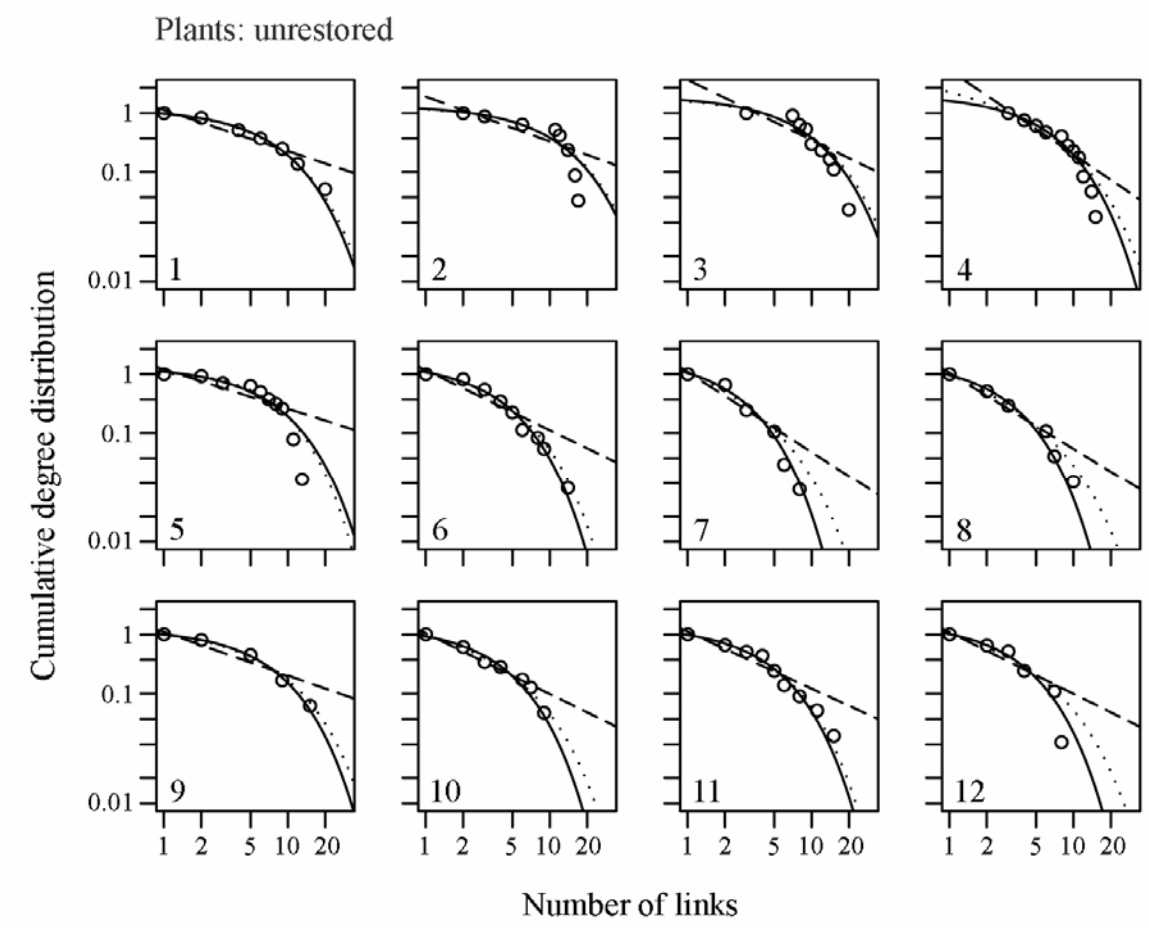
APPENDIX XI continued



APPENDIX XI continued



APPENDIX XI continued



CURRICULUM VITAE

Name	Kaiser
First name	Christopher Niels
Date/City of Birth	26th July 1976 in Bonn, Germany
Nationality	German

EDUCATION

1986 – 1995	Helmholtz-Gymnasium, Bonn, Germany
1996 – 1999	Studies of Biological Sciences and Geography, University of Bonn, Germany
1999 – 2000	ERASMUS scholarship: University of East Anglia, UK
2000 – 2002	Biological Sciences, University of Bonn, Germany Graduation: Diploma Thesis: Influence of wind and pollen gathering by bees on reproductive success of the tropical grass *Brachiaria platynota* K. Schum. (Poaceae: Paniceae) at Kakamega Forest Nature Reserve, Kenya
2002 – 2006	Ph.D. at the Institute of Environmental Sciences, University of Zurich Supervisors: Prof. C. B. Müller and Dr. J. Memmott (University of Bristol)